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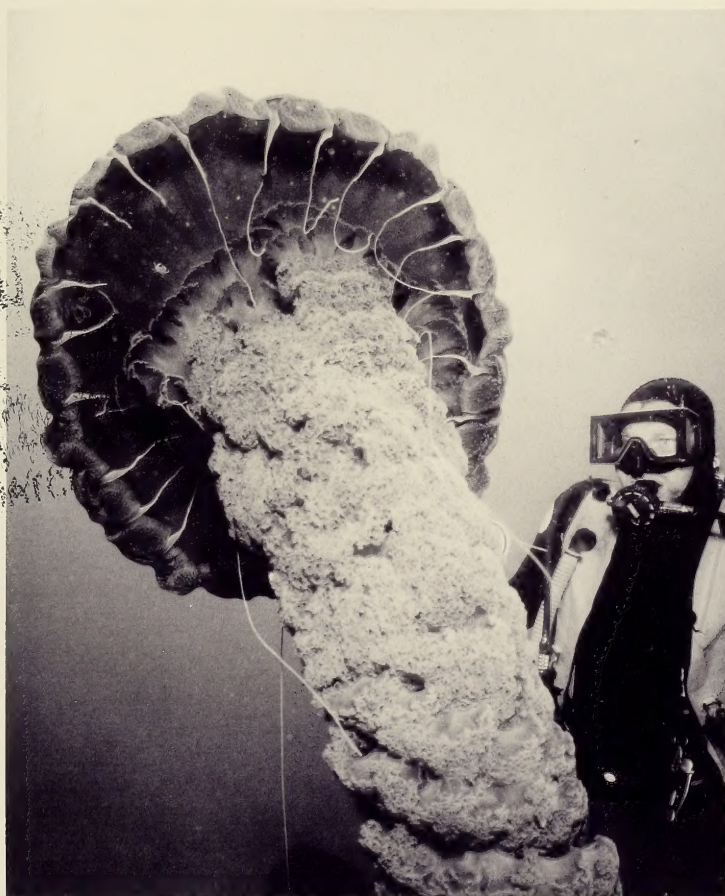
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THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

**Faunal Associates of an Undescribed Species of *Chrysaora*
(Cnidaria, Scyphozoa) in the Southern California Bight,
with Notes on Unusual Occurrences of Other Warm Water
Species in the Area**

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Abstract.—A large, undescribed species of scyphomedusa (Cnidaria, Scyphozoa) was sighted offshore, in bays, and washed up in large numbers on beaches of Southern California and northern Baja California, México, during the summer of 1989. Invertebrate associates, taken from two living but damaged medusae lacking tentacles and oral arms, included a pycnogonid sea spider and two species of mysidacean shrimp not previously reported associated with scyphozoans. These species probably became attached as the moribund medusae contacted the seafloor prior to washing ashore. Previously reported scyphozoan associates included a hyperiid amphipod and larval (megalopal) and juvenile brachyuran crabs of the genus *Cancer*. Photographs and video footage of living scyphomedusae allowed observations of the natural history of the medusae and of the behavior of juvenile crabs. The unique occurrence of this scyphozoan and its faunal associates is described and discussed along with other unusual local occurrences of species from other, mostly tropical, regions.

From July 7 through early September 1989, unidentified dark purple scyphozoan medusae were sighted along the eastern Pacific coast from at least as far south as Isla San Martín, off San Quintín, Baja California, México, north to Santa Monica Beach, California. The medusae were found in greatest numbers washed ashore on sand beaches and in the surf zone within 100 m from shore but were also sighted from boats traveling in bays and to approximately 1 nautical mile offshore (Table 1). Offshore medusae were all observed at the surface with the exception of one sighting at a depth of 21 m (above the wreck of the *Olympic* off Long Beach, California, Table 1) and the medusae filmed off the Islas de Los Coronados (see below). Most medusae in the above sightings were approximately 20 to 40 cm in bell diameter. Additionally, photographs and video footage (provided by Howard Hall and Mark Conlin, of Howard Hall Productions) showed a "school" of larger specimens (estimated bell diameter up to 1 m; Figs. 1, 2) from Coronado Norte, Islas de Los Coronados, Baja California, México.

Distinguishing characteristics of those scyphomedusae washed ashore or observed nearshore include a light brown to tan reticulated pattern about 3 to 8 cm wide surrounding the dorsal perimeter of the bell (Figs. 1A, B), a dark purple mesoglea, a dark red-brown mucous that is produced when the medusae are handled (see Shanks and Graham 1988, for description of mucous production as a defensive mechanism in living scyphomedusae), and a mild sting. Living spec-

Table 1. Collecting (*) and sighting localities of undescribed species of *Chrysaora* (Cnidaria, Scyphozoa) in 1989. Medusae that harbored invertebrate associates (**). Abbreviations under "Proximity to Shore" are: O = offshore; B = bay; I = inshore (near shore); S = stranded (onshore).

Locality	Proximity to shore	Date
Isla San Martin, San Quentin, Baja California, Mexico		
D. Montagne	O	07 July 1989
Coronado Norte, Islas de Los Coronados, Baja California, Mexico		
H. Hall and M. Conlin	O/I	09, 26, 31 July 1989
Los Angeles Breakwater Light, Long Beach, CA**		
M. Curtis	O	15 July 1989
Desmond Bridge, Long Beach, CA		
E. Mastro and T. Deckel	B	27 July 1989
Desmond Bridge, Long Beach, CA*		
E. Mastro and T. Deckel	B	28 July 1989
Santa Monica Beach, CA		
J. Seigel	S	12 August 1989
Dana Point, CA		
B. Ormsby	B	15 August 1989
Venice Beach, CA**		
B. Hogue and D. Golles	I	20 August 1989
Venice Beach, CA*		
J. Martin and H. Kuck	I/S	25 August 1989
Venice Beach, CA**		
R. Feeney et al.	I	25 August 1989
San Diego, CA		
D. Pasko and D. Zmarzly	B	30 August 1989
Venice Beach, CA		
T. Rudnick	I/S	late August 1989
Venice Beach, CA*		
R. Fay	I	late August 1989
Estero Beach, Ensenada, Baja California, Mexico		
R. Fox	I	late August 1989
La Jolla, CA		
R. McConnaughey	O	early September 1989
Scripps Inst. of Oceanography Pier, La Jolla, CA*		
R. Snodgrass	I	early September 1989
Torrey Pines Fish & Game Reef, La Jolla, CA		
R. Snodgrass	O	early September 1989

imens, found mostly offshore, additionally have delicate tentacles and thick oral arms extending approximately 6 m (estimated from photographs and video footage, Figs. 1, 2). The tentacles and oral arms were missing from specimens that were sighted near shore or had washed ashore, with the exception of one specimen sighted but not collected off Long Beach, California (Table 1). The phenomenon was discussed with regional biologists and local residents, none of whom had seen this species before. Dr. Ron Larson, Harbor Beach Oceanographic Institution, Inc., Fort Pierce, Florida, determined, after examination of our specimens, other specimens, and the video footage of living animals, that the scyphomedusa is an undescribed species of the semaeostome genus *Chrysaora* (Larson 1990 and in preparation). In this paper we discuss the invertebrates and fish seen or collected

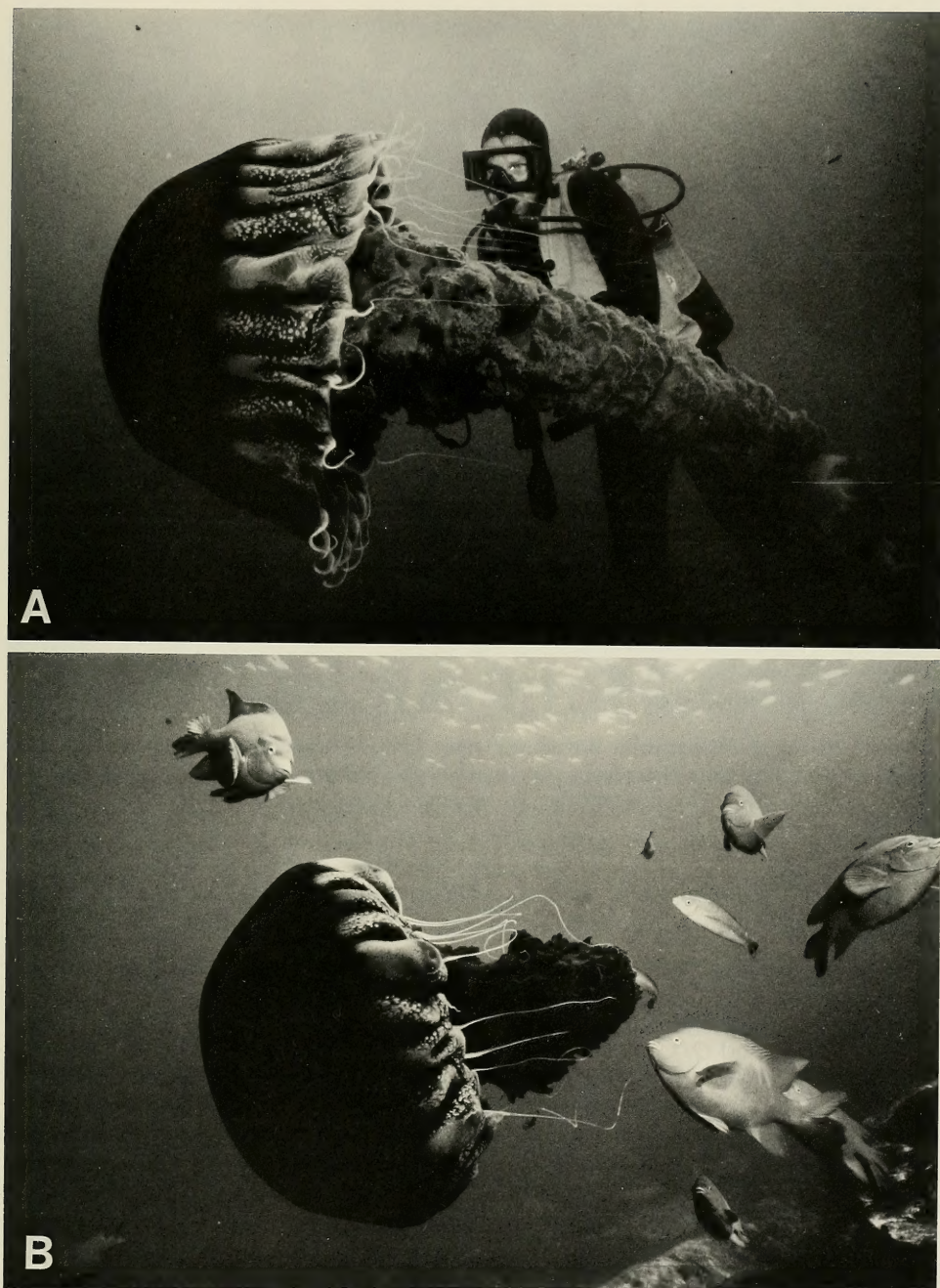


Fig. 1. In situ photographs of new species of purple jellyfish, *Chrysaora* sp., taken by members of Howard Hall film crew off Coronado Norte, Islas de Los Coronados, northern Baja California, México, July, 1989. A, intact medusa in front of diver; bell diameter estimated at 1 m. Note length of tentacles and especially oral arms, estimated to 6 m, which trail to bottom right of photograph (and terminate beyond frame of photograph). B, medusa with damaged tentacles and oral arms near seafloor. Note garibaldi and senioritas possibly feeding on oral arms and tentacles, probably explaining in part why only the bell exists in stranded specimens.

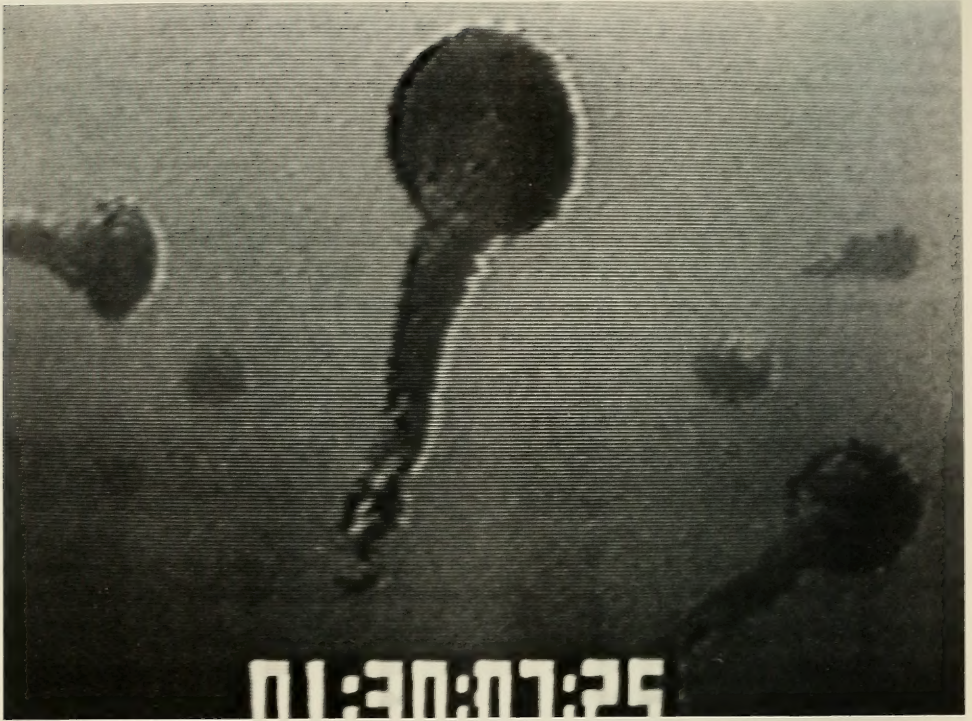


Fig. 2. Photograph of "school" of medusae, taken from video monitor, showing density of the jellyfish off Coronado Norte, Islas de Los Coronados, Baja California, México, July, 1989. At least 7 animals are in the field of view, 3 on either side of central largest (closest) animal.

in association with this new species. Additionally, we discuss this unusual occurrence in light of other unusual species occurrences in the area.

Materials and Methods

The first scyphomedusa specimen seen by us was collected on 20 August 1989 by B. T. Hogue and D. Golles, both lifeguards at Venice Beach with over 43 years combined experience (8 Hogue, 35 Golles) in the area without having seen this species. This large (approximately 23 cm bell diameter) living medusa was collected approximately 100 m offshore of Venice Beach, California. The medusa was donated to the Natural History Museum of Los Angeles County (LACM) and was brought to our attention because of the number of juvenile brachyuran crabs found on the manubrium (oral arms) and subumbrellar surface of the bell; it was subsequently catalogued as LACM 89-206.1 An additional live specimen (LACM 89-205.1, bell diameter approximately 25 cm) was collected on 25 August 1989 by the LACM Ichthyology Section just north of the Marina del Ray jetty, Venice, California. The authors counted another 24 dead specimens washed ashore along Venice Beach on 25 August 1989 and collected one dead specimen (LACM 89-26.1, bell diameter approximately 24 cm) floating on the surface in the surf zone. Another dead specimen (bell diameter approximately 22 cm) was collected by staff members of the Cabrillo Marine Museum near Long Beach, California (Table

1). The two live specimens and the two dead specimens were washed with warm tap water over a sieve (U.S. Standard #10; 0.5 mm mesh size), and invertebrates were collected from the washings. Three of the above specimens, and all collected invertebrate associates, were deposited at LACM; the fourth is housed at the Cabrillo Marine Museum, San Pedro, California (CMM Acc. No. 89.28.1). Additional observations of living medusae and associated fish were gleaned from video footage supplied by Howard Hall Productions.

Results

Invertebrate Associates

Neither of the dead medusae harbored any invertebrate associates. The two living medusa, both from off Venice Beach, Venice, California, harbored a variety of invertebrates, listed below. Because all of the symbionts were washed off in order to collect them we could not determine where on the medusa they were originally located.

Pycnogonida

Family Callipallenidae

Anoropallene palpida (Hilton, 1939)

One female with swollen femorae containing eggs, total length (tip of proboscis to end of abdomen) 2.6 mm, leg span 7.2 mm (LACM 89-205.4).

Remarks: This species is fairly common from Southern California south to Panama (Brusca 1980) but has never been reported in association with a scyphozoan or other cnidarian host, nor has it been found in a parasitic association with any other species (C. Allan Child, pers. comm.). Child (pers. comm.) has collected in Panama "over 100 of this species [*A. palpida*] from a sterile-appearing mud substrate with almost no epifauna on which they could feed." In fact there are very few reports of any association between pycnogonids and pelagic cnidarians, although benthic cnidarians are common prey items (Mauchline 1984; Child and Harbison 1986). The appendages do not appear to be specialized for clinging to a cnidarian host (compared to, for example, the appendages of species of the genus *Pallenopsis*; C. Allan Child, pers. comm.), and it is possible that this specimen attached itself to the jellyfish as the weakened medusa came in contact with the seafloor.

Crustacea, Amphipoda

Family Hyperiididae

Hyperia medusarum (Muller, 1776)

One female, total length 8.1 mm (LACM 89-206.2).

Remarks: Hyperiidids are common associates of planktonic medusae and were reviewed by Thurston (1977), Harbison et al. (1977), and Laval (1980). Almost all reported hosts for the genus *Hyperia* are scyphozoan medusae, with the exceptions being ctenophores and one "dubious report" with a salp (Laval 1980: 15, see also Madin and Harbison 1977) and at least some hydromedusae (Pasko 1987). Laval (1980) questioned the reliability of records of associations with ctenophores; it is likely that species of *Hyperia* occur only on scyphozoan and hydrozoan medusae (Pasko 1987). There are 8 or 9 currently recognized species in the genus, depending upon whether the two "forms" of *H. medusarum*, *hystrix*

form and *medusarum* form, are treated as subspecies of *H. medusarum* or are recognized as distinct species (Bowman 1973). In Southern California the *hystrix* form is most commonly encountered (Bowman 1973), although the form we collected was *medusarum* (Gary Brusca, pers. comm.). Records of *H. medusarum* as associates of medusae in Southern California are numerous, and it is not surprising to encounter this species on any large scyphozoan host (Thurston 1977; Laval 1980; Pasko 1987; Gary Brusca, pers. comm.).

Crustacea, Mysidacea

Family Mysidae

Metamysidopsis elongata (Holmes, 1895)

2 adult males, total length of both approximately 4.7 mm (LACM 89-205.2).

Mysidopsis cathengela Gleye, 1982

1 adult male, total length 10.5 mm; carapace length 2.8 mm (LACM 89-205.3)

Remarks: *Metamysidopsis elongata* is common in Southern California waters, and was the most abundant nearshore (to 36 m depth) mysid encountered in studies off San Onofre, California (Linda Gleye, unpub. data). Off La Jolla, California, the species can be "so abundant immediately above the bottom that vision of divers is obscured" (Clarke 1971). *Mysidopsis cathengela* was described in 1982 from San Onofre State Beach, California, and is morphologically similar to *Mysidopsis californica* (Gleye 1982).

Although several mysid species are associated with benthic cnidarians, such as the mysid *Heteromysis actiniae* on the sea anemone *Bartholomea annulata* (Clarke 1955), we are not aware of any previous reportings of mysids as associates of scyphozoans (Linda Gleye and Ron Larson, pers. comm.). Because both species are abundant near shore and particularly near the bottom for *M. elongata*, it seems likely that these mysids became associated with the medusae only as the latter approached shore.

Crustacea, Brachyura

Family Cancridae

Cancer sp. (cf. *C. antennarius* Stimpson, 1856)

Twelve juveniles, all apparently belonging to the same species, ranging in size from carapace width (CW) of 3.1 to 22.1 mm. Eleven larvae (megalopae), from CW of 1.6 to 2.8 mm (LACM 89-206.3, 8 juveniles and 4 megalopae, from medusa LACM 89-206.1; LACM 89-205.5, 4 juveniles and 7 megalopae, from medusa LACM 89-205.1).

Remarks: The largest and most numerous associates of the jellyfish were juvenile crabs of the genus *Cancer*. The largest of these (CW 22.1 mm) was a male. The other 11 juvenile specimens ranged from CW of 3.1 mm to 18.1 mm; three were males, one was female, and the other seven specimens were too small to allow assessment of sex. Of the latter, two specimens of about 8.0 mm CW had sexual characteristics of both sexes (i.e., gonopores on the third abdominal sternites and two pairs of gonopods). A crab was seen but not collected on the medusa sighted at 21 m depth off Long Beach, California (Table 1), and also on at least one of the medusae photographed by the Howard Hall film crew off Islas de Los Coronados, Baja California, México (Fig. 3).

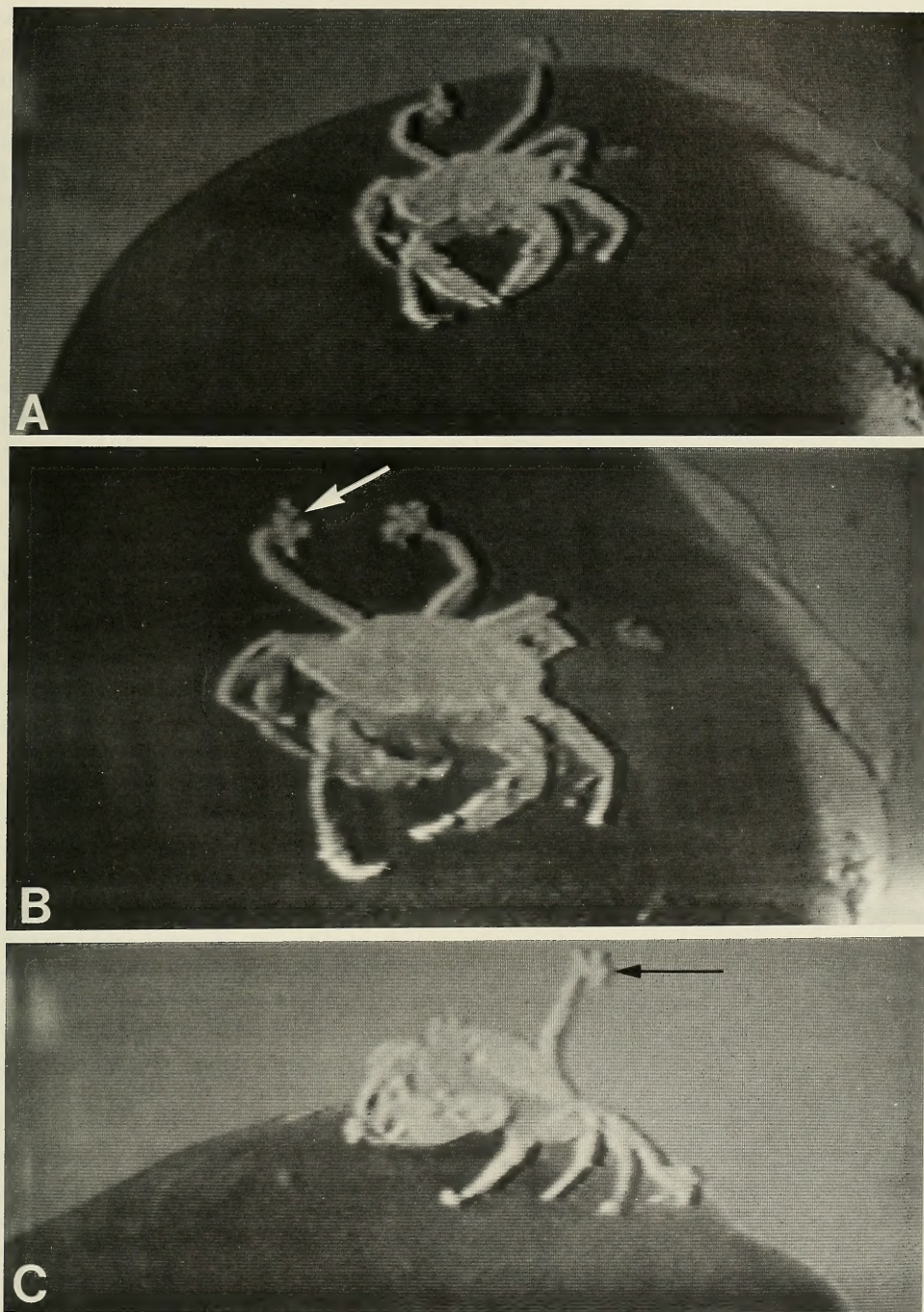


Fig. 3. Large specimen of juvenile or subadult *Cancer* sp. on medusa (photographs taken from video monitor). A, crab on exumbrellar surface of bell. B, slightly higher magnification of same animal showing clusters of foreign material (white arrow) adhering to dactylus of both fifth pereiopods; note also dactylus of other pereiopods embedded in medusa. C, side view of same animal in A and B showing elevated fifth pereiopod on right side (arrow) during a "shaking bout" (see Discussion).

There are approximately 14 species of *Cancer* known from the west coasts of North and South America (Nations 1975; Carvacho 1989a, b). Only 6 of these—*C. amphioetus*, *C. antennarius*, *C. anthonyi*, *C. branneri*, *C. gracilis*, and *C. jordani*—are common in Southern California (Nations 1975). However, if these medusae originated in more southern waters, as we suspect (see Discussion), then the crab associates could belong to a more southern species, such as *C. porteri* or *C. johngarthi* from México and Central America (see Carvacho 1989a, b). Nations (1975) divided extant and fossil species of *Cancer* into 4 subgenera based primarily on characters of the carapace. Following his subgeneric diagnoses the largest specimen of ours can be placed in the subgenus *Romaleon* (based on the development, curvature, and spination of the anterolateral teeth of the carapace), to which only 3 of the above-mentioned species—*C. branneri*, *C. antennarius*, and *C. jordani*—belong. Using Nation's (1975) characters, which were based on adult morphology, we tentatively identified these juveniles as belonging to *C. antennarius* Stimpson, 1856. However, little is known concerning ontogenetic changes of the characters of the carapace, and *C. gracilis* is more commonly known as a medusa associate (W. M. Graham, pers. comm.), so our identification of juveniles as *C. antennarius* should be accepted with caution.

In addition to the juveniles, there were several megalopae, also attributable to the genus *Cancer*. The megalopae bear well developed spines on the ischium of the cheliped and on the coxa of the second walking leg; in this respect the megalopae are similar to those of several other species of the genus (Quintana and Saelzer 1986; DeBrosse et al. 1990), but are not attributable to *C. gracilis* according to the recent key to megalopal stages of species of *Cancer* by DeBrosse et al. (1990). That key is restricted to 4 northwest coast species and does not include *C. antennarius*. However, the table of characters presented by Quintana and Saelzer (1986), for which information on *C. antennarius* was taken from the description by Roesijadi (1976), is useful for identifying megalopae in Southern California. The megalopae taken from the medusae differ from those tabulated in Quintana and Saelzer (1986: 294) in that they are slightly smaller and less setose on some of the mouthparts.

The size of one of the *Cancer* crabs seen in the video footage (not collected), and its behavior, are worth noting. The crab appears to be larger than any of the specimens we collected and is probably a subadult. Attached to the dactyli of the fifth pereopods (walking legs) are clusters of foreign matter that are conspicuous even at low video resolution (Fig. 3) (see Discussion).

Vertebrate Associates

Osteichthyes

Family Stromateidae

Peprilus simillimus (Ayres, 1860) (Pacific butterfish)

Several specimens, apparently adults, estimated size 10-15 cm, observed on video footage only.

Remarks: This was the only fish species observed in association with the medusae while they were healthy and offshore. All butterfish were observed swimming rapidly behind the bell and in close proximity to the oral arms, and they maintained this position throughout the video segment. Once the medusae began to

weaken and drag across the sea floor, other fish were evident from the video footage (Fig. 1B). Garibaldi (*Hypsypops rubicundus*) apparently were feeding on the now-disintegrating jellyfish, or possibly on plankton on the tentacles and oral arms (W. and P. Hamner, pers. comm.), although proximity of the scyphomedusae to the seafloor also may have evoked a territorial response in the adult males (R. Lavenberg, pers. comm.). Other fish, such as senorita (*Oxyjulis californica*) and blacksmith (*Chromis punctipinnis*), also were seen in the vicinity of the disintegrating medusae and may have been feeding on associates of the medusae or on small pieces of the oral arms.

Discussion

Although the scyphozoan medusae that appeared in 1989 belong to an undescribed species, these sightings are not the first. According to R. Larson (pers. comm.), a photograph of what is undoubtedly the same species appeared in the August, 1926, issue of *National Geographic* (Crowder 1926: 190). The photograph was labelled only "black jellyfish" and had no indication of where it was taken. Another photograph of this species appeared in Halstead (1965, vol. 1: plate XLIII); however, the species was incorrectly identified as *Cyanea capillata* and the photograph was attributed to the western Atlantic (Florida) rather than the Pacific, which is possibly an error. It is also possible that the new species has occurred in waters off Southern California before but was overlooked or was misidentified as *Pelagia colorata*, although this seems unlikely in light of the differences in color patterns (Larson 1990: fig. 3C). The new scyphomedusa is the fourth known species of *Chrysaora* from the eastern Pacific (Larson 1990).

Several observations suggest that the medusae originated from waters to the south of the area where they came ashore. The first confirmed sightings (early July, 1989; Table 1) were from northern Baja California, México, and it was not until later that month that the first records were made further north, in Southern California. Additionally, the video footage that showed large numbers of living medusae (Fig. 2) indicates that both numbers and condition declined as the medusae came inshore. It is likely that as the medusae came northward and into shallower waters, fish and macroinvertebrates began to remove portions of the oral arms and tentacles, with the result that only the bell was intact in the two living animals seen by us and in the many stranded specimens encountered along Southern California beaches.

Scyphozoan medusae are known to undergo long-term population fluctuations. The best documented case is that of *Pelagia noctiluca* in the western Mediterranean Sea, where records extending back 200 years show population blooms approximately every 12 years (Goy et al. 1989). It is doubtful that the appearance of the dark purple medusae in 1989 along Southern California beaches reflects a bloom of a species that is otherwise rare. That this species has not been reported from Southern California despite the fact that these beaches are so heavily populated and relatively well known biologically suggests that the medusa does not normally occur in this geographic area.

There have been other unusual occurrences along California beaches of species not normally encountered in this geographic area. Humboldt squid (*Dosidicus gigas*) occasionally come ashore (approximately every 35 to 40 yr; Kerstitch 1989) in large numbers during the grunion (*Leuresthes tenuis*) breeding months, and

have become stranded on Southern California beaches at least twice in the mid to late 1970s (Suzanne Lawrenz-Miller, pers. comm. and Kerstitch 1989); a large "squid slick" inundated the beaches at Dana Point and Laguna Beach, California, as this paper was being prepared, and the story was carried by local newspapers (The Orange Coast Daily Pilot, 4 August 1990; and Orange County edition of the Los Angeles Times, 3 and 4 August, 1990). There has been at least one stranding of another cnidarian, the siphonophore *Verella vellella*, which came ashore in large numbers during the mid to late 1970s (Wickham 1976; Charles Galt, pers. comm.). *Verella* has been reported to harbor megalopal stages of at least two species of *Cancer* (*C. magister* and another unidentified species; see Wickham 1976). Perhaps the best documented large scale influx of any species in Southern California involves the red galatheid squat lobster, *Pleuroncodes planipes*, which occurs in great numbers during or immediately following an El Niño event (Glynn 1961; Boyd 1967; T. Parker, pers. comm.).

The spectacular 1982–1983 El Niño event was the strongest recorded for this century. Sea surface temperatures were as much as 8°C above normal in the western Pacific; the Pacific Equatorial Current reversed direction and extended eastward for 8000 miles to the coasts of North, Central and South America (Canby 1984; Wooster and Fluharty 1985). Among the unusual faunal distributions resulting from this oceanic-atmospheric phenomenon were reports of barracudas off the coast of Oregon, loss of cold-water salmon in the Pacific northwest, and tropical vertebrates and invertebrates along western coasts of North and South America. It would seem unlikely that the occurrence in 1989 of previously unseen medusae could result from an El Niño event 6 years earlier. There is also a possibility that this occurrence might be a harbinger of an upcoming El Niño event; one precursor of El Niño in Chile is the occurrence of large numbers of a related jellyfish (*Chrysaora plocamia*; see Soto 1985), but as of early 1991 there has been no indication of a forthcoming El Niño event.

The invertebrate associates of the scyphozoan can be grouped into two categories. The hyperiid amphipod, and the megalopal and juvenile stages of the brachyuran crabs, often have been reported as associates of pelagic medusae, and their presence on the new scyphozoan is not surprising. It is perhaps surprising that only one hyperiid and so few crabs were found on four rather large medusae, but the four specimens we sampled, only two of which were still living at the time, were in poor condition. It seems reasonable to expect more hyperiids on a healthy specimen with tentacles and oral arms intact. The pycnogonid and the two mysids are more interesting finds. There are no previous reports of these species on pelagic medusae, and there are no morphological specializations of the pycnogonid that would suggest an association with a medusa (C. Allan Child, pers. comm.). These taxa probably can be considered "accidentals," most likely having become associated with the scyphozoans after the latter began to come ashore. Future sampling of intact medusae would help to answer this question.

The range in size of the juvenile crabs and the presence of megalopal stages suggest that there are no discrete size classes as have been found in other scyphozoan/crab associations (W. M. Graham, pers. comm.). The presence of these larvae and juveniles also suggests that the crabs are dispersing via the jellyfish, as has been found in northern populations of *Cancer* on a congeneric species of scyphozoan, *Chrysaora fuscescens* (in Graham 1989, as *C. melanaster*). The oc-

currence of decapod Crustacea on medusae is not unprecedented and indeed there are larval forms among the Decapoda that have been hypothesized to be modified just for such an existence (e.g., the phyllosoma stages of spiny lobsters: Shojima 1963; Thomas 1963; Herrnkind et al. 1976). Association with pelagic organisms is only one of several behaviors exhibited by decapod larvae to facilitate dispersal (e.g., see Shanks 1986).

The behavior of the brachyuran crab in the video footage (Fig. 3) is curious. As previously noted, there were clusters of foreign matter on the dactyli of the posterior (fifth) pereopods. The crab appeared to hold these appendages off the dorsal surface of the bell at the same time that all other pereopods had their dactyli slightly embedded into the bell for grasping. From time to time the crab shook these back legs (Fig. 3C), but whether this behavior was for balance or was an attempt to dislodge the foreign matter on the dactylus, or served some other purpose, was not clear. We also do not know the nature of these clusters of material, although they appear in texture to be similar to the more flocculent borders of the jellyfish's oral arms and may be no more than adhering mucous balls from that part of the medusa. Another suggestion is that the foreign matter on the dactyli are clusters of nematocyst-bearing tissue from the oral arms of the medusa (W. and P. Hamner, pers. comm.). If so, there is the possibility that some defensive benefit to the crab exists, and the behavior may have been elicited by the presence of the photographer. We can not yet speculate as to the significance of the "shaking bouts" that the crab displays. Other crabs were seen on the video to actively ingest strands of detritous-laden mucous from the oral arms of the jellyfish, so that at least one benefit to the crab of the association seems to be nourishment.

As far as we know, there were no abnormal conditions of temperature, salinity, air pressure, upwellings, or other physical factors in the summer of 1989 (D. Pasko, pers. comm., and Climate Diagnostics Bulletin (NOAA), February–October 1989). As of this writing (February 1991), we know of no further sightings of the medusae along Southern California or Baja California, México.

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Addendum

The following publication, which contains a synopsis of scyphomedusae from the waters of California and mentions the *Chrysaora* n. sp. upon which the present paper is based, came to our attention too late to be incorporated into the text.

Larson, R.J. and A.C. Arneson. 1990. Two medusae new to the coast of California: *Carybdea marsupialis* (Linnaeus, 1758), a cubomedusa and *Phyllorhiza punctata* von Lendenfeld, 1884, a rhizostome scyphomedusa. *Bull. S. Calif. Acad. Sci.*, 89(3):130–136.

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Behavioral Ecology of the Banded Rock Lizard (*Petrosaurus mearnsi*)

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Abstract.—Two populations of *Petrosaurus mearnsi* were studied in southern San Diego County, California. Home range size calculations found those of females larger than those of males ($\bar{x}$ = 98.5 m², $\bar{x}$ = 86.5 m²). Home range and observational data suggest that the species does not exhibit the home range defense typical of most iguanid lizards. *P. mearnsi*, like most southwestern iguanids, exhibits highest activity in late morning during cooler months becoming bimodal during the heat of the summer. Activity patterns of individual lizards were found to be very irregular. Feeding behavior is described and diet analysis confirms the species as being insectivorous, favoring dipteran and hymenopteran prey. Social behavior is examined and note made of the lack of knowledge about reproductive behavior. Some data are presented on growth, survivorship, and reproduction.

The banded rock lizard (*Petrosaurus mearnsi*) inhabits large granitic boulders and cliffs primarily on the desert side of the peninsular mountain ranges of southern California and Baja California as far south as 28°30'N Lat. (Fig. 1). The range of *Petrosaurus thalassinus repens* overlaps the southern 130 km of the range of *P. mearnsi*. Generally *P. mearnsi* in this area inhabits the Gulf side of the peninsula while *P. t. repens* inhabits the backbone of the peninsula. There is an approximately 50 km stretch of this region in which the two species are sympatric (Murphy 1983). The purpose of this study was to investigate some of the biotic and abiotic factors which influence home range, diet, interactions with other species, and reproductive behavior by comparing several ecological parameters in two populations at the extremes of its altitudinal range.

Methods

This study was conducted during 1978 and 1979 for a total of 552 hours on 50 days.

Study Areas

The first study area was along the desert edge of the In-Ko-Pah Mountains at Dos Cabezas Siding, San Diego County, California (Lat. 32°44'50"; Long. 115°08'00"; elev. 507.68 m). Dos Cabezas is a granodiorite boulder region, with the larger foothills reaching 75–150 m above the desert floor. The desert floor is coarse to fine sand derived from decomposing granodiorite. This site was selected because it was accessible by vehicle but isolated and within Anza-Borrego State Park. It contained some isolated boulder outcrops which had resident *Petrosaurus* populations that could be fairly easily observed. One such isolated outcrop, 50 m × 36 m, with a population of 9–12 lizards, served as the main study population.

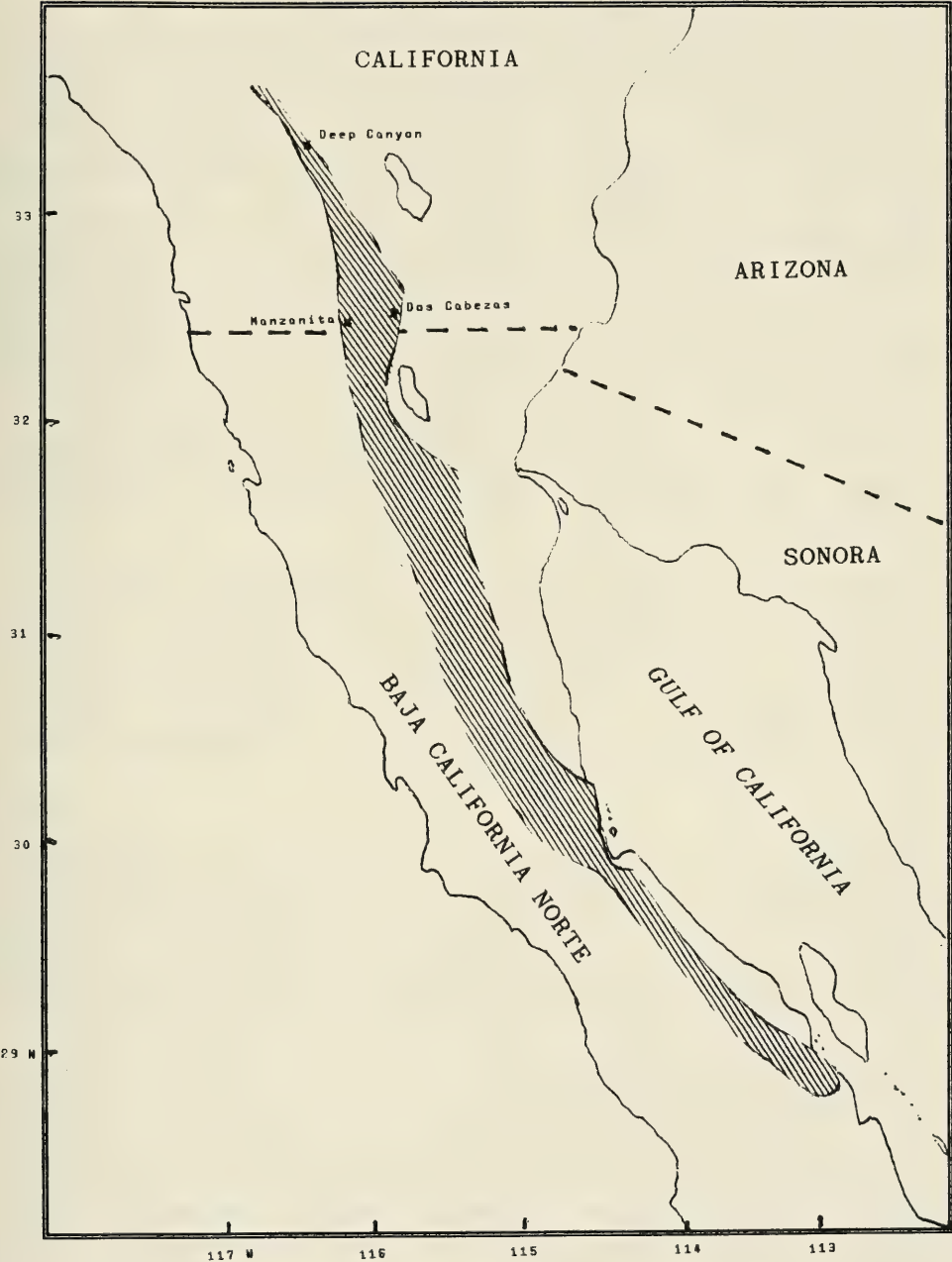


Fig. 1. Range of the banded rock lizard, *Petrosaurus mearnsi*.

The relative isolation of the outcrop reduced emigration and immigration. *P. mearnsi* was rarely seen to cross open ground between boulders. In captive enclosures, they readily cross the ground from one boulder pile to another a meter apart.

The plant life of this area consists of the Colorado Desert division of the Sonoran

Desert cactus scrub community (Burk 1977). Common perennials include Bigelow cholla (*Opuntia bigelovii*), beavertail cactus (*Opuntia basilaris*), barrel cactus (*Echinocactus acanthodes*), creosote (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), chuparosa (*Beloperone californica*), indigo bush (*Dalea californica*), burrow weed (*Ambrosia dumosa*) and rose mallow (*Sphaeralcea rosacea*). In March and April of years with good winter rains the desert floor and the spaces between boulders are covered with a variety of herbaceous plants.

The second study area was 3.7 km east of Manzanita, San Diego County, California (Lat. 32°40'05"; Long. 116°17'25"; elev. 995.6 m), in a narrow, north-south trending valley. The valley walls average 90 m above the floor and consist of boulders and outcrops of granodiorite. The study population occupied a 54 m long, semi-isolated section of the east wall of the canyon, with boulders reaching 6 m in height. Approximately 10 lizards occupied this outcrop. It was not as isolated as the Dos Cabezas site and more emigration and immigration were noted. The soil is mainly derived from the granodiorite and contains a fair amount of organic matter. This site was chosen as the second study area because of its high elevation near the upper limit for *P. mearnsi*, and for its security on privately owned, fenced land.

The plant life of this area is open mixed California chaparral (Hanes 1977). Common perennials include red shank (*Adenostoma sparsifolium*), manzanita (*Arctostaphylos* spp.), sugarbush (*Rhus ovata*), scrub oak (*Quercus dumosa*), mountain lilac (*Ceanothus* spp.), chamise (*Adenostoma fasciculatum*), holly leaf cherry (*Prunus ilicifolia*), pale sliktassel (*Garrya flavescens*), and desert tea (*Ephedra californica*). The valley floor is dominated by grasses, some annual herbaceous plants, and scattered live oaks (*Quercus agrifolia*).

Field Observations

Observations were made 2-8 days each month from March through October, 1978, and again for the same months in 1979. Some random observations of hibernation were made in December, 1977, and again in December, 1978. Twelve animals were captured by noosing at Dos Cabezas and seven at Manzanita. Lizards were toe clipped for permanent identification, and marked with a fluorescent paint spot on the dorsum for field observation identification. Since no marked lizards disappeared from the Dos Cabezas during the observation season, it is assumed the paint did not affect survivability.

The following data were collected for all marked lizards: daily activity patterns; sex; S-V length at each capture and recapture; display behaviors; body, air, and rock temperatures at each capture and recapture with a Schultheis Rapid-recording Thermometer. Home range was calculated by noting the position on a map of each marked lizard each time it was observed. Home range size was estimated using the minimum polygon method.

Ten lizards from sites adjacent to the study plots were shot with a pellet gun and stomach contents analyzed.

Results

Activity Patterns and Thermoregulation

Seasonal

At Dos Cabezas, lizards emerge from inactivity in mid to late February and are active on warm, clear days. During March lizards emerge between 0730-0830

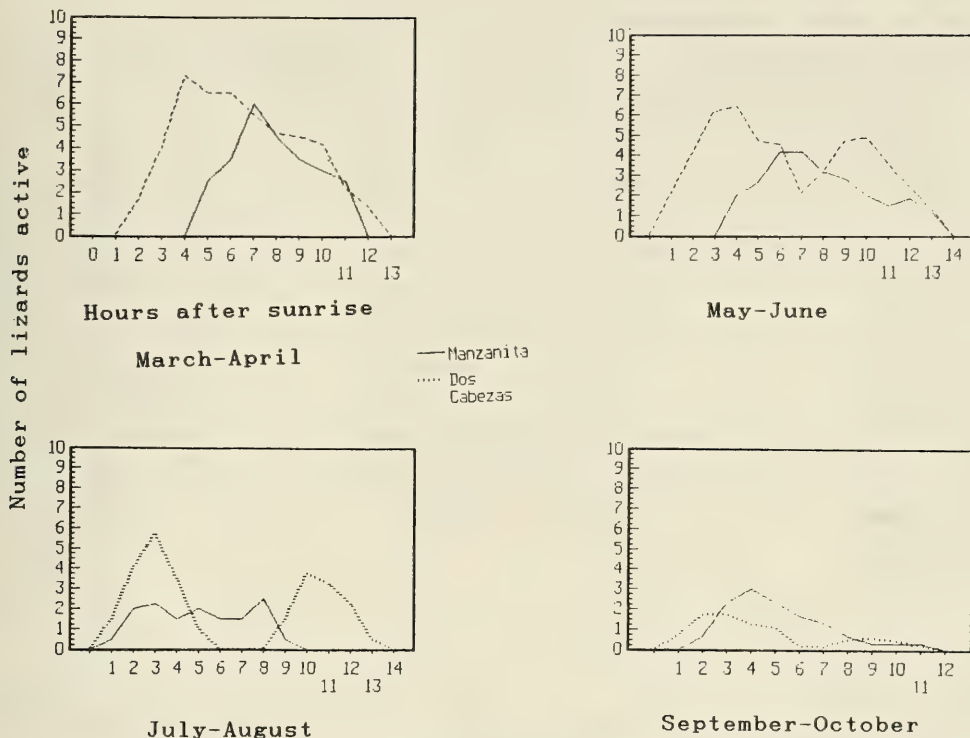


Fig. 2. Average daily activity of *P. mearnsi* in southern San Diego County, California (N = 12 D, 10 M).

hrs at air temperatures of 15–25°C. Substrate temperatures vary only a degree or two from air temperatures at this time. Lizards bask for 20–30 minutes, then begin feeding, moving around their home range and interacting with conspecifics. By 1500 hrs most lizards have retired and those that are left are thymothermically absorbing heat from the rocks which are now 34–38°C. Air temperatures are 22–28°C. By 1600 hrs all lizards have disappeared into crevices (Fig. 2).

April activity is much the same as March, except that emergence averages 15 minutes earlier. May is warmer and emergence (0600–0630 PST) is within 30 minutes of sunrise. When air and rock temperatures have risen to 32–35°C and 38–45°C, respectively, in early afternoon, the lizards retreat to their crevices.

By mid June a distinctly bi-modal activity pattern is seen. Lizards come out within a few minutes of sunrise (c. 0500 hrs) and remain active until late morning when air and rock temperatures exceed 32–37°C and 42–50° respectively. During the latter part of the morning most activity takes place on the shady sides of the boulders. In late afternoon there is another lesser period of activity. By mid-July the mid-day inactive period has lengthened to about 5 hours and only a few lizards reappear in late afternoon.

By August activity is brief and limited to the early morning. There is an apparent exception to this for a few days following a heavy summer rain when the activity reverts to mid-June levels.

September and October show a slight increase in overall activity period, if newly hatched juveniles are included. However, few adults are active during these months

Table 1. Example of daily activity pattern of two individual *Petrosaurus mearnsi*.

Male, Dos Cabezas, 1978		Female, Manzanita, 1979	
Date	Approx. activity period	Date	Approx. activity period
3/27	0900-0925 (when captured)	4/27	1000-1030 (when captured)
3/28	0900-1300	5/8	1000-1300
4/25	0800-1200	5/22	0900-1100
4/26	0800-1100	5/23	0900-1100
5/6	0800-0900	6/15	not seen
5/7	not seen	6/16	0800-1200
6/12	not seen	6/17	0900-1000
6/13	1500-1700	7/4	not seen
7/5	not seen	7/7	not seen
7/6	not seen	8/2	1700-1800
7/7	0700-0800	8/3	not seen
8/3	0800-1000	9/6	1000-1100
8/4	0800-1000	9/7	not seen
8/5	not seen	10/9	not seen
9/8	0900-1000		
9/9	0900-1000		
10/7	not seen		
10/8	not seen		

and by the end of October almost all activity ceases, although an occasional lizard may be out in mid-morning.

At Manzanita, *Petrosaurus* does not emerge from hibernation until late March. Activity is sporadic until late April. At this elevation weekly cold weather fronts can drop temperatures 10 degrees from one day to the next in April. By early May the activity period at Manzanita resembles that of Dos Cabezas a month earlier. Lizards first appear about 0800 when the air temperature is about 20°C. The study site (a west-facing cliff) does not receive much sun in April until 1100 hrs. Activity lasts until well into the afternoon, gradually diminishing after 1500 hrs, with some lizards still basking at sunset. The bimodal activity pattern does not begin in Manzanita until early July. By early August activity at Manzanita, like Dos Cabezas, is limited to a few early morning hours. Few adult lizards are active in September, and by early October all activity has ceased.

The minimum air temperature with activity recorded was 10°C; the maximum 38°.

Individual Activity

The observation of marked animals revealed a remarkable irregularity in activity patterns of individual lizards as contrasted with the population as a whole (Table 1). Individual lizards were sometimes active in the morning, sometimes in the afternoon, and rarely were bimodal, even though the population as a whole shows such bimodal pattern during the summer months. Some days individuals were not active at all. During ecdysis inactivity was the rule. Most females showed several days of inactivity during June, presumably near the time of oviposition.

When lizards are active they continually shuttle back and forth from the shady side of a boulder or crack to the sunny side.

Table 2. Activity index of lizards at noon. Activity index = no. of observed lizards divided by the total number of marked lizards.

Dos Cabezas, 1978			Manzanita, 1979		
Date	12 noon air temp. °C	Activity index I = n/o	Date	12 noon air temp. °C	Activity index I = n/o
3/27	28	.50	4/24	18	.00
3/28	28	.42	4/27	22	.43
4/25	33	.58	5/8	25	.86
4/26	34	.58	5/22	27	.71
5/6	32	.33	5/23	27	.71
5/7	33	.33	6/15	31	.57
5/20	35	.25	6/16	30	.43
5/21	37	.33	6/17	31	.57
6/12	35	.33	7/4	35	.43
6/13	35	.25	7/7	36	.29
6/14	38	.16	8/2	36	.43
7/5	38	.00	8/6	36	.57
7/6	40	.00	9/6	38	.14
8/4	45	.00	9/7	38	.29
8/5	45	.00	10/9	25	.00
9/8	39	.00			
9/9	38	.00			
10/7	32	.08			
10/8	30	.08			

Cloacal temperatures of lizards which have completed basking and begun feeding or other activity ranged from 34°C to 37°C. Table 2 correlates activity with air temperature at noon on specified days.

Inactivity

A study of the boulder habitat of *Petrosaurus* during the winter months (November–January) revealed that many, but not all, *P. mearnsi* use down-facing exfoliations of the granodiorite as hibernacula. As many as five *Petrosaurus* have been found in a single crevice, which is also often shared with *Xantusia henshawi* and *Phyllodactylus xanti* at Dos Cabezas and with *X. henshawi* and *Urosaurus microscutatus* at Manzanita. *Petrosaurus* does not use exfoliations during the active months. Nocturnal refuges of all marked lizards were deep horizontal or vertical cracks in the rocks. Marked lizards (N = 22) were noted to use the same crack each night 85% of the time.

Food and Feeding Behavior

P. mearnsi is a sit-and-wait forager, albeit a restless one. An individual lizard will sit motionless on a boulder until an insect lights a few centimeters from it. It then typically rises on its legs bringing its body forward to grab the insect with its mouth. If the insect is farther away, the lizard will sometimes chase it, especially if it is a beetle or ant. Lizards seldom used the same spot for hunting insects for more than 2 or 3 minutes, changing positions frequently.

During the peak spring months when the shrubs and herbs at the base of the boulders are in bloom, *Petrosaurus* has a special foraging behavior. The plants

Table 3. Summary of stomach contents of 10 *Petrosaurus mearnsi* from Dos Cabezas, San Diego Co., California, May 1979.

Prey category	Number	Volume cc	% total number	% total volume	Frequency (no. of stomachs)
Insecta					
Hymenoptera					
Apidae	15	2.00	19	25	8
Formicidae	23	0.50	29	6	4
Other	6	0.50	8	6	5
Diptera	13	1.25	16	15	8
Coleoptera	5	0.50	6	6	5
Lepidoptera					
larvae	4	0.60	5	7	2
adults	2	0.40	2	5	1
Hemiptera	2	0.20	2	2	2
Orthoptera	2	0.80	2	10	1
Arachnida					
Araneida	7	1.20	9	15	5
Reptilia					
<i>X. hemshawii</i> (juv.)	1	0.40	1	5	1
Plant material	—	0.15	—	2	1

attract flying insects and the lizards cling to the boulders (often on the vertical plane) and jump out and seize insects as they light on the flowers. The lizards then climb off the plant and back on the boulder again. In fact, this is almost the only time this species leaves a rock surface.

Feeding occurs chiefly in the morning hours. Foraging has been observed as early as 0730 and lizards usually stop foraging by 1100 hrs. Occasionally foraging is seen in the afternoon and has been seen on the west-facing cliff at Manzanita as late as 1800 hrs.

Insects are the primary food, based on 20 lizards, 10 from near each study site, taken 5/7/79 (Dos Cabezas) and 5/22/79 (Manzanita) (Tables 3 and 4). Plant material occurred in 10% of the stomachs of Dos Cabezas specimens and in 30% of those from Manzanita. Small pieces (<2 mm) of granodiorite were found in many stomachs (84%).

In captivity *Petrosaurus* will readily eat small lizards. The stomach of one individual in the Dos Cabezas population contained a small *Xantusia henshawi*.

Home Range

Careful observations of marked lizards indicate that *P. mearnsi* does not have a true center of activity for the home range. Some lizards use one part of their range for a few days, then another; others have a center of activity for the morning hours and another for the afternoon. This prevents use of the probability density function to determine home range size.

The habitat of *P. mearnsi* presents another problem. It consists at both sites of large boulders with open spaces between them. Most boulders are situated so that

Table 4. Summary of stomach contents of 10 *Petrosaurus mearnsi* from Manzanita, San Diego Co., California, June 1979.

Prey category	Number	Volume cc	% total number	% total volume	Frequency (no. of stomachs)
Insecta					
Hymenoptera					
Apidae	7	1.50	10	35	4
Formicidae	34	0.50	48	12	5
Other	2	0.25	3	6	2
Diptera	5	0.50	7	12	5
Coleoptera	11	1.75	15	41	7
Lepidoptera					
larvae	4	0.60	6	14	2
adults	1	0.20	1	5	1
Hemiptera	4	0.40	6	9	2
Orthoptera	1	0.30	1	7	1
Arachnida					
Araneida	2	0.30	3	7	2
Plant material	—	0.40	—	10	3

lizards can roam over four to five sides; some are so perched as to present most of six sides. *P. mearnsi* are able to scamper across granitic surfaces on the vertical and even upside down. There is no known practical method of assessing this multidimensional component of home range (Milstead 1971). However, it would seem that the unmodified minimum polygon method (using the formula of Jennrich and Turner 1969) is the best measurement of home range size, keeping in mind that it seriously underestimates the actual surface covered by a particular lizard. Home range sizes of marked lizards at both sites are presented in Figures 3 and 4.

Home range areas are summarized by sex and study site in Figures 5 and 6. Home ranges of males (N = 7) ranged from 25–165 m² with a mean of 86.5 m²; females (N = 7) ranged from 69–198.5 m² with a mean of 98.5 m². Home range size of adult lizards (N = 7) at Dos Cabezas had a mean of 103 m², at Manzanita (N = 7) the mean was 81 m². There was considerable overlap of home ranges of both sexes at both study sites.

Density

Although the numbers are small, the maximum density (on a two-dimensional basis) at Dos Cabezas is 66/h; at Manzanita 300/h. Hain (1965) found densities of 160–3300/h in Deep Canyon, Riverside Co.

Social Behavior

Intraspecific Behavior

Several hundred displays were observed, and 60 of them quantified and detailed. Only 20 of these were directed at conspecifics. Most displays appear to be spontaneous, with no evident object in view. These were the assertion displays de-

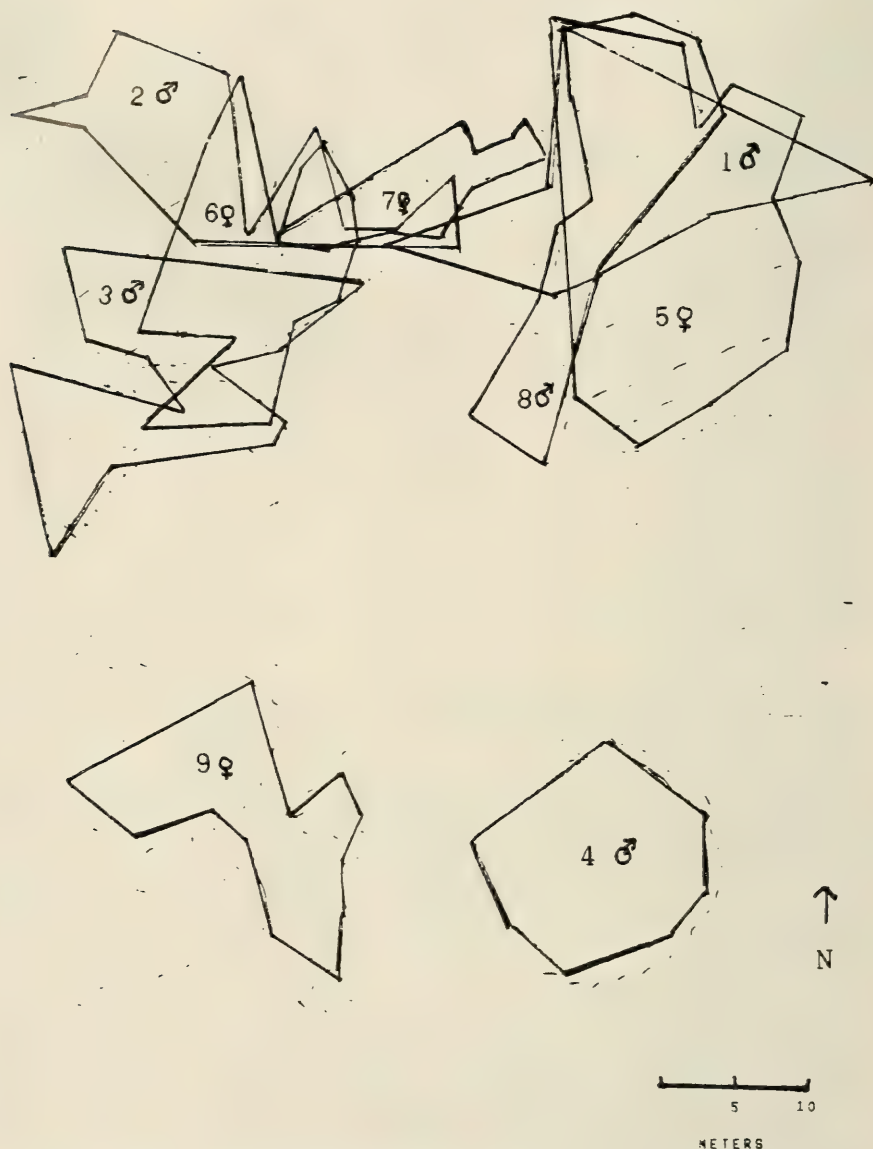


Fig. 3. Graph of home ranges of nine lizards (*P. mearnsi*) at Dos Cabezas in 1978.

scribed by Carpenter (1962). At Dos Cabezas and Manzanita 55% of the displays consisted of two units of 3–9 ($\bar{x} = 4.5$) pushups; 45% were of one unit. Carpenter (1962) and MacKay (1975) mention only two unit displays; Cozens (1978) saw only one unit displays at Manzanita. The pushups decline in height during a unit and involve alternating flexion and extension of the front legs while the back legs remain flexed. Immatures and females display, but 77% of the displays studied in marked lizards were by males. Displays occurred in all months that lizards were active, and there was no significant difference by season.

The 20 displays directed at conspecifics occurred when another lizard (sex not significant) approached closer than 0.5–0.75 m. Following such displays the small-

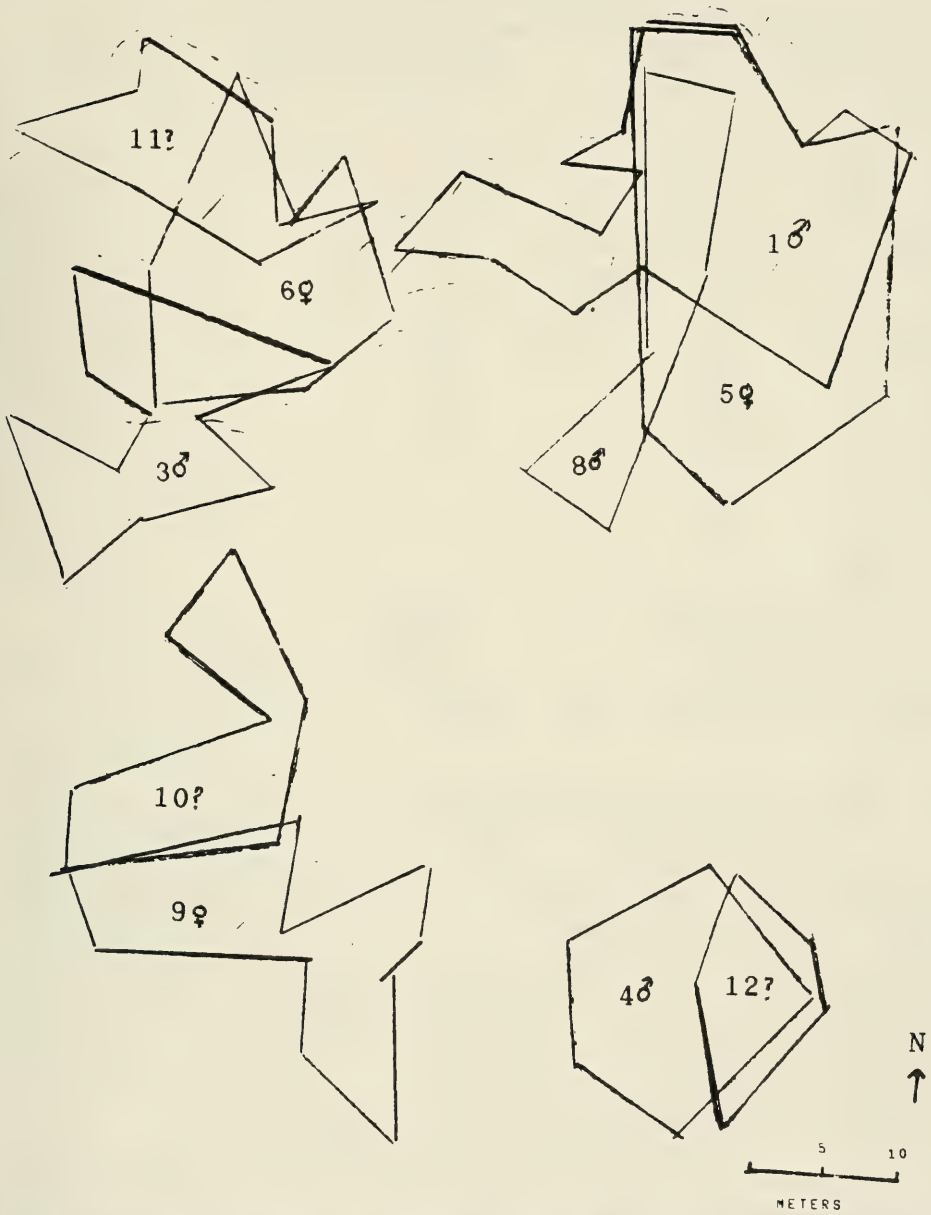


Fig. 4. Graph of home ranges of ten lizards (*P. mearnsi*) at Dos Cabezas in 1979. Where numbers are the same as in Fig. 11, lizards are the same individuals.

er lizard in the encounter usually moved away; if it did not it was chased a short distance. No physical contact between lizards was ever seen. No extensions of the dewlap or lateral compression, typical of many sceloporines, were ever observed in *Petrosaurus*.

Interspecific Behavior

Sceloporus orcutti, *Uta stansburiana*, and *Sauromalus obesus* share the same microhabitat and activity period with *P. mearnsi* at Dos Cabezas. *S. orcutti*, *S.*



Fig. 5. Home range size of *Petrosaurus mearnsi* in southern San Diego County, California. Vertical lines indicate ranges, horizontal lines indicate means, numbers above indicate sample sizes.

occidentalis, *Uta stansburiana*, and *Urosaurus microscutatus* share the same habitat at Manzanita. *Xantusia henshawi* shares the same habitat at both sites, but not the same activity period; *Phyllodactylus xanti* occurs in crevices at Dos Cabezas but is active nocturnally. Although several of these species (especially *Uta*) were frequently seen within a meter of *P. mearnsi*, only two interspecific encounters with behavioral components were observed. One, at Dos Cabezas, involved *S. obesus*. The *Petrosaurus* was sitting on top of a boulder when the chuckwalla emerged from its crevice and moved toward the top of the rock. The rock lizard moved away to the side of the boulder. No displays were made by either lizard. The second encounter occurred at Manzanita when an *Uta* was noted on top of a boulder as a *Petrosaurus* approached. The *Uta* displayed twice, and then gave way to the rock lizard, which made no display.

S. orcutti have home ranges which greatly overlap the ranges of *Petrosaurus* at Dos Cabezas, but they seldom encounter each other. *S. orcutti* appears to forage mostly on the ground around the boulders, and uses the boulders only for basking. It is an earlier riser than *P. mearnsi*, and no interspecific behavior was seen.

Growth and Survivorship

At Dos Cabezas a total of nine lizards were caught and marked in the spring. Only one of these disappeared before the end of October. Six additional hatchlings were caught in September and October, 1978, and marked. By March, 1979, one adult male and three of the hatchlings had disappeared, leaving ten lizards that were followed without further loss until September, 1979. Increase in snout-vent length of field marked animals is presented in Table 5. Survivorship over the 17 month period 1978-1979 is summarized in Table 6.

Relative tail breaks have been widely used to evaluate predation in lizards by

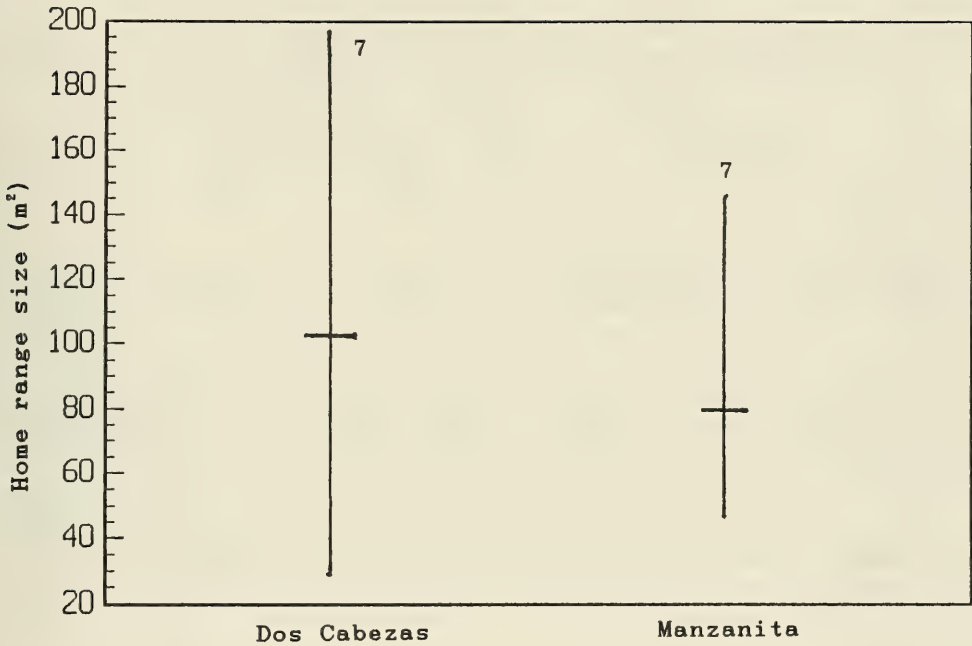


Fig. 6. Comparative home range size of adults of two populations of *P. mearnsi* in southern San Diego County, California. Vertical lines indicate ranges, horizontal lines indicate means, numbers above indicate sample sizes.

Parker and Pianka (1973), Vitt (1974), Schall and Pianka (1980) and many others, although Vitt and Cooper (1986) question the assumptions behind this. A remarkable observation in the Dos Cabezas population was the total absence of any broken or regenerated tails. This is not simply a bias of the marked lizard sample size. During reconnaissance of neighboring rocky outcrops several dozen *Petrosaurus* were sighted and not one was missing a tail. A few lizards with broken tails were seen in the Manzanita area. The only dead rock lizard ever seen was one mummified adult found in a crevice that I opened. The only possible diurnal predators seen during this study in the Dos Cabezas area were the raven *Corvus corax* and the shrike *Lanius ludovicianus*. *Crotalus mitchelli* is a known lizard predator which is also present. No *Masticophis* were seen in the vicinity of Dos Cabezas, although they are quite common at Manzanita.

Sex Ratio

Of the 39 *P. mearnsi* collected during this study which could be sexed, 22 were females and 17 were males, giving a sex ratio of 1.29 females for 1.0 males. This does not differ significantly from 1:1 ($P > 0.05$). Hain (1965) found an almost identical sex ratio of 1.0 males to 1.3 females ($N = 103$) in his Deep Canyon study; and Cozens (1978) found a sex ratio of 1.2 males to 1.0 females ($N = 69$) in his study at Manzanita.

Sexual Dimorphism

The only consistently reliable method of distinguishing sex on live lizards was the enlarged postanal scales in males. This agrees with statements by Sloan (1967), Stebbins (1954), and Cozens (1978). Adult males averaged longer (S-V) than adult

Table 5. Growth of 12 *Petrosaurus mearnsi* at Dos Cabezas, 1978–1979.

	No.	S–V length (mm)		No. intervening months		S–V increase (mm)		Increase/month (mm)	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Adult males	4	84.5	78–89	15.75	14–17	2.25	0–8	0.14	0–0.5
Adult females	3	78	76–79	14.66	14–15	2.66	2–4	0.18	0.13–0.29
Immat. males	1	53	—	16	—	25	—	1.56	—
Immat. females	1	54	—	2	—	9	—	4.50	—
Juveniles	3	36.5	35–38	11.75	11.5–12	32	28–35	2.72	2.3–3.18

females (84.5 to 78 mm). Both sexes have blue-gray patches on the sides of the ventrum and under the chin. Darker or lighter coloration in these patches is not a reliable indicator of sex, but appears to be correlated to body size with the largest (> 75 mm) lizards usually having the darkest ventral color. Of course, there are more males in this size class. Hain (1965) stated that “only the bright reddish tip of the male’s nose distinguished the sexes.” None of the *P. mearnsi* in southern San Diego Co. seem to have such sexual dichromatism in nose color.

Clutch Size

Twelve of the 20 lizards collected for food studies were females. Of the nine over 75 mm SVL, eight contained enlarged ovarian ova, numbering 1–4, averaging 2. Hain (1965) indicates egg laying occurs in late June–early July in desert edge populations. Cozens (1978) indicates egg laying about a month later for the mountain populations.

Discussion

Activity Periods

There is no clear evidence to explain the irregular daily activity patterns exhibited by all the marked lizards in this study. Nutritional state may possibly play some role, with lizards remaining in their crevices on days after successful feeding periods. The summer air temperatures would probably be high enough to promote digestion without basking.

The sharing of crevices by several lizards during the winter is a behavior not shown during the active season. At first it was thought the crevices under exfoliated rock might be warmer, at least on sunny days, than deep crevices, and thus attract several lizards. Then some lizards were discovered under exfoliations that were in perpetual shade. This behavior may be a predator-avoidance strategy, as the crevices are totally inaccessible to any vertebrate predators.

Feeding Behavior

In this study and that of Cozens (1978) lizards were never seen foraging on the ground, although Hain (1965) says they do so in Deep Canyon. Only four lizards were seen on the ground during the two years of this study, and they were only crossing short distances (< 1 m) between boulders. A straight line may be the shortest distance between two points, but *Petrosaurus* will almost always go the long way around to avoid leaving a rock surface.

Table 6. Age-specific survivorship 1978–1979 (17 months, N = 12).

Survivorship interval	
Egg to first year	.50
Adult males	.80
Adult females	.75

Cozens (1978) thought that plants are an important part of the diet of *P. mearnsi*. Experiments with captive animals, however, have failed to get them to eat vegetable matter. It may be that the plant material found in stomach contents is due to accidental ingestion consequent to the foraging behavior around flowering plants described above. However, Vitt (pers. comm.) doubts that the ingestion is accidental. Parker and Pianka (1973) found a similar frequency of plant material in the stomachs of *Sceloporus magister*, and Mayhew (1963) found wild mustard flowers in *S. orcutti*, which is sympatric with *P. mearnsi* at both study sites of this investigation.

The small pieces of granodiorite found in many stomachs may also be accidentally ingested when lizards grab insects from rocky surfaces. Again, Cozens (1978) thought these pebbles to be of importance in mechanical digestion.

Home Range and Territoriality

Hain (1965) states that *P. mearnsi* “is definitely territorial. In all major areas of observation, a specific territory was shared by a mature male and mature female. Immature individuals were not paired and did not defend any specific territory.” His discussion further on, including measurements of such territories seems to indicate he equates territories and home ranges. He does not define “territory” in his paper. MacKay (1975) also states that *P. mearnsi* is “territorial as are the majority of iguanid lizards” and describes the assertion display mentioned previously as the total extent of defense of territory. MacKay used Rand’s (1967) definition: “a territory is an area of space within which a particular individual dominates a certain category of intruders who dominate it elsewhere.” In spite of MacKay’s citation of this definition, in his calculation of home ranges he shows two males with completely overlapping home ranges. However, one reviewer says that these males used different parts of the home range at different times of day and thus showed some exclusivity. Noble (1939) simply defined a territory as “any defended area.” Both Rand’s and Noble’s definitions are a bit vague to be useful in lizard ecology. A territory to truly be such must be actively defended by the presence of the owner. Stamps (1977) distinguishes two types of territoriality: *Home range defense*, in which essentially the whole home range is actively defended and equates with territory; *Specific site defense*, in which only a small area of the home range is defended. Home range defense by adult males is the usual pattern found in most iguanid lizards (Stamps 1977), and as understood by MacKay (above). *P. mearnsi* is certainly not territorial in this sense, at least in southern San Diego Co., as is evident from the study of Cozens (1978) and the present one. On four occasions at Dos Cabezas males #5 and #8 were observed in the overlap zone, visible to each other, but with 0.75–1 m distance intervening. However, as pointed out by Tinkle (1969) and others the degree and type of

territoriality may vary from population to population within a species, especially with changes in habitat. There is considerable difference in habitat structure between the high canyon wall habitat in the northeastern part of the range of *P. mearnsi* and the rather open boulder outcrop habitat over most of the rest of its range.

Stamps (1977) accepts as evidence of the second type of territoriality "exclusive occupancy of the 'site'" (or small area), "extensive to complete overlaps of the rest of the home range and evidence of active defense of the site." She defines *non-territorial* as defending no portion of the home range, with no exclusive occupancy sites and no defense of any area. The study of the Dos Cabezas and Manzanita populations, and perhaps also the Deep Canyon population indicate that *P. mearnsi* actually exhibits a kind of specific site defense. The several hundred hours of observations at Dos Cabezas and Manzanita indicate that *P. mearnsi* does defend a "site," but only the one it is occupying at the moment, about one meter in diameter. It pays little attention to other lizards passing to and fro through its home range if they stay a half meter or more away from its present location. There is not even any evidence of tolerance of subordinates within that defended zone, with larger lizards chasing smaller, males chasing females. MacKay (1975) also found a lack of subordinate tolerance. Since *P. mearnsi* seldom stays in one "site" very long, this defended area is constantly shifting.

Cozens (1978) puzzled over this seeming contradiction between his observations and the strong claim to territoriality by Hain (1965) and MacKay (1975). He thought that *P. mearnsi* might have a dominance hierarchy at Manzanita. A limited peck-right hierarchy (Stamps 1977) could be said to exist in the San Diego County populations of *P. mearnsi* in so far as the largest lizard does dominate smaller individuals within the home range overlap zones. These overlap zones are so limited, however, that there would just be a two step hierarchy at the densities (60–300/h) of populations in San Diego County.

Good visibility is considered a prime requisite for territoriality (Stamps 1977). It is possible that the complex geometry of the boulder habitat of *P. mearnsi* may have prevented the more typical iguanid territoriality from evolving in this species. In typical *P. mearnsi* habitat only a small portion of a lizard's home range (estimated 5–20%) is visible to the lizard from any one site within the range.

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Subspecies Limits and Geographic Patterns of Morphological Variation in California Gnatcatchers (*Polioptila californica*)

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Abstract.—California Gnatcatchers (*Polioptila californica*) are distributed from the arid coastal plain of southern California south throughout most of the lowland regions of Baja California. Atwood (1988) suggested that populations in central Baja California were not subspecifically distinct from populations occurring north of 30°N latitude, and that the range of the northern, nominate subspecies therefore extended south to the Cape region of the peninsula. However, re-examination of data used in the earlier analysis indicates that the primary break in patterns of morphological variation in California Gnatcatchers occurs near 30°N, and that populations north of this latitude are subspecifically distinguishable from populations occurring in central Baja California. Patterns of variation south of 30°N latitude are less clearly defined, with variably distinct steps in clinal variation exhibited by different characters near 28°N and/or 24°N latitude. Multivariate analyses indicate that in central and southern Baja California the principal break in morphological variation occurs near 24° N latitude. Following these results, the naming and distributions of subspecies of *Polioptila californica* should revert to that initially proposed by Grinnell (1926): *P. c. californica* (north of 30°N), *P. c. margaritae* (from 30°N south to 24°N), and *P. c. abbreviata* (south of 24°N).

The California Gnatcatcher (*Polioptila californica*) was recently recognized as being specifically distinct from the Black-tailed Gnatcatcher (*P. melanura*) of the Sonoran and Chihuahuan deserts (Atwood 1988, American Ornithologists' Union 1989). In the United States, California Gnatcatchers are restricted to the arid coastal plain of southern California, where they occur in remnant patches of coastal sage scrub located below 2000 feet elevation (Atwood 1980, 1988). The species' distribution also includes most of the lowland, arid regions of Baja California (Atwood 1988).

Although I have already presented some information concerning geographic patterns of morphological variation in California Gnatcatchers (Atwood 1988), most of those data were analyzed in the context of interspecific comparisons with two other species, *Polioptila melanura* and *Polioptila nigriceps*. Because my primary emphasis was on among-species differences, I must concur with the criticisms of Johnson (1989) and Banks (1989) that details of intraspecific variation in *Polioptila* are difficult to assess from data provided in Atwood (1988). Here I further examine geographic patterns of variation in *Polioptila californica*, and discuss the implications of such patterns on the delineation of subspecific limits.

Methods

A total of 212 study skins of male California Gnatcatchers were used to analyze patterns of geographic variation; sample sizes of females from several areas of

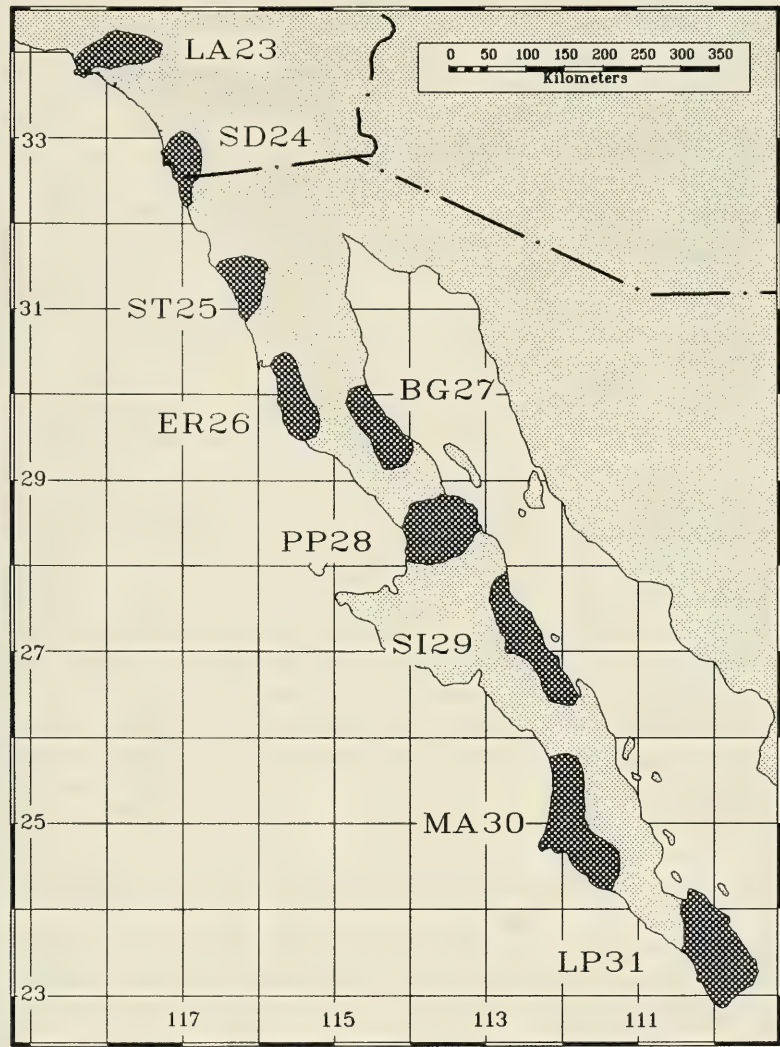


Fig. 1. Location of sample areas used in analysis of California Gnatcatcher morphological variation. For specific collecting localities, see Atwood (1988).

Baja California were too small to warrant inclusion of this sex. Specimens were grouped into 9 sample areas along a latitudinal gradient from southern California to the tip of Baja California (Fig. 1); specific localities included within each sampling area are given in Atwood (1988). I used specimens from sample area LA23 to assess the possible influence of collection date (month) on each of the morphological measurements described below. Because Wilcoxon 2-sample tests failed to identify significant ($P < 0.05$) differences between fresh-plumaged specimens collected during September–December ($N = 30$) and more worn specimens obtained during January–April ($N = 27$), I combined specimens taken during different months for the subsequent analyses of geographic variation (Table 1).

Atwood (1988) described methods used to obtain measurements of major body elements, feather lengths, and plumage coloration. In this analysis I use the fol-

Table 1. Collection dates and sample sizes of specimens used in analysis of geographic variation in *Polioptila californica*.

Area ^a	Total	Month of collection					
		Jan–Feb	Mar–Apr	May–Jun	Jul–Aug	Sep–Oct	Nov–Dec
LA23	60	11	16	0	3	15	15
SD24	27	10	5	1	0	8	3
ST25	16	0	3	0	0	2	11
ER26	19	8	7	0	0	3	1
BG27	14	8	4	0	0	2	0
PP28	14	5	5	0	0	2	2
SI29	19	3	10	4	0	2	0
MA30	15	7	6	2	0	0	0
LP31	28	16	10	0	0	0	2

^a Sample areas as shown in Fig. 1.

lowing morphological characters (abbreviations provided in parentheses): bill length (BLEN), bill width (BWID), bill depth (BDEP), length of tarsus + length of middle toe (TARTOE), length of primaries 3–10 (P3–P10LEN), tail length (TLEN), length of rectrices 4–6 (R4–R6LEN), length of rectrices 4–6 expressed as percent of total tail length (R4–R6PCT), length of terminal white spots on rectrices 5 and 6 (R5–6SL), length of terminal white spots on rectrices 5 and 6, expressed as percent of total tail length (R5–R6SPCT), amount of white on outer vane of rectrices 5 and 6 expressed as percent of total vane (R5–6WEB), spectrophotometric brightness values of breast and back plumage (BRSTB and BACKB), spectrophotometric purity values of breast and back plumage (BRSTP and BACKP), and dominant wavelength of breast and back plumage (BRSTW and BACKW). A single categorical variable, the shape of the terminal white spots on rectrices 5 and 6 (R5–6SSH), was also used in one analysis for the sake of comparison with Atwood (1988).

Analyses were performed using SAS (Version 6.06) procedures CLUSTER, GLM, MEANS, NPARIWAY, STEPDISC, TREE, and VARCLUS. For parametric tests, log 10 and arcsin transformations were performed on measurement and percentage variables, respectively.

Results

Seven major clusters of intercorrelated variables were identified by oblique centroid cluster analysis of the correlation matrix of 31 characters. Components of these clusters were: (1) P3–10LEN, TLEN, R4–6LEN, R4PCT; (2) BRSTB, BACKB, R5–6SL, R5–6SPCT, R5–6PCT, R5–6WEB; (3) BRSTW, BACKW, BACKP; (4) BWID, BDEP; (5) BRSTP; (6) TARTOE; and (7) BLEN. Because the geographic patterns of variation exhibited by characters belonging to each cluster were redundant, I present only selected examples in the following discussion.

The 13 characters included in Cluster 1 showed little variation from 34°N south to approximately 28°30'N. In measurements associated with tail length, a relatively pronounced step occurred between 28°30' and 27°N latitude (Fig. 2a); wing length measurements showed a less obvious step between 27°N and 25°N (Fig. 2b). The 10 components of Cluster 2 had little variation from 34°N south to a

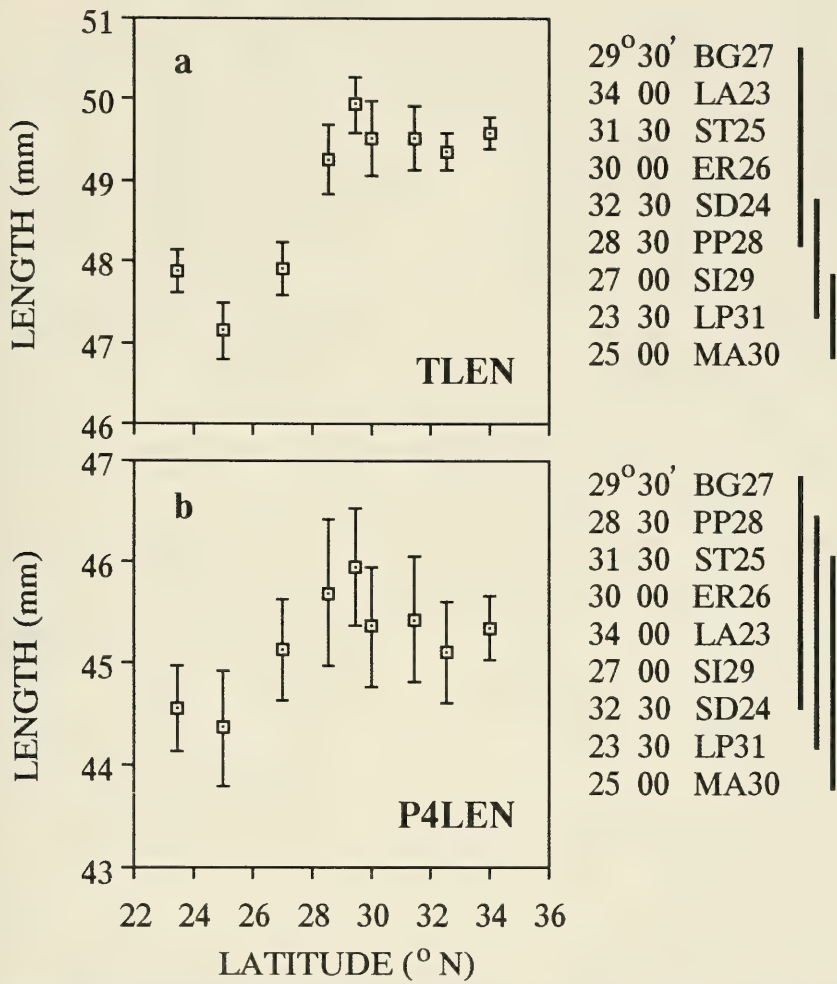


Fig. 2. Examples of geographic variation in characters included in Cluster 1 (P3-10LEN, TLEN, R4-6LEN, R4PCT). Character abbreviations as given in Methods. Plots indicate mean $\pm$ 1 standard errors. Vertical bars to right of each plot connect homogeneous subsets determined using Gabriel's (1978) multiple comparison technique; latitudes of each sample area (degrees, minutes) are listed in descending order of their means.

variably distinct break located between 31°30' and 30°N latitude (Fig. 3a, b); south of 30°N, these characters varied clinally, with a secondary step in the pattern of variation occurring between 25°N and 23°30'N latitude. The 3 variables included in Cluster 3 showed little variation from 34° south to 31°30'; a sharp step occurred between 31°30' and 30°N latitude (Fig. 3c). In specimens obtained from sample area BG27 (29°30'N latitude), characteristics of variables assigned to Cluster 3 resembled those of areas farther north (Fig. 3c), possibly as a result of character displacement in this region where *Poliioptila californica* occurs sympatrically with *Poliioptila melanura* (Atwood 1988). Characteristics of variables included in Cluster 3 were relatively constant south of 29°30'N latitude. Clusters 5 (BRSTP) and 6 (TARTOE) each varied clinally from 34° south to approximately 28°30'N (Fig.

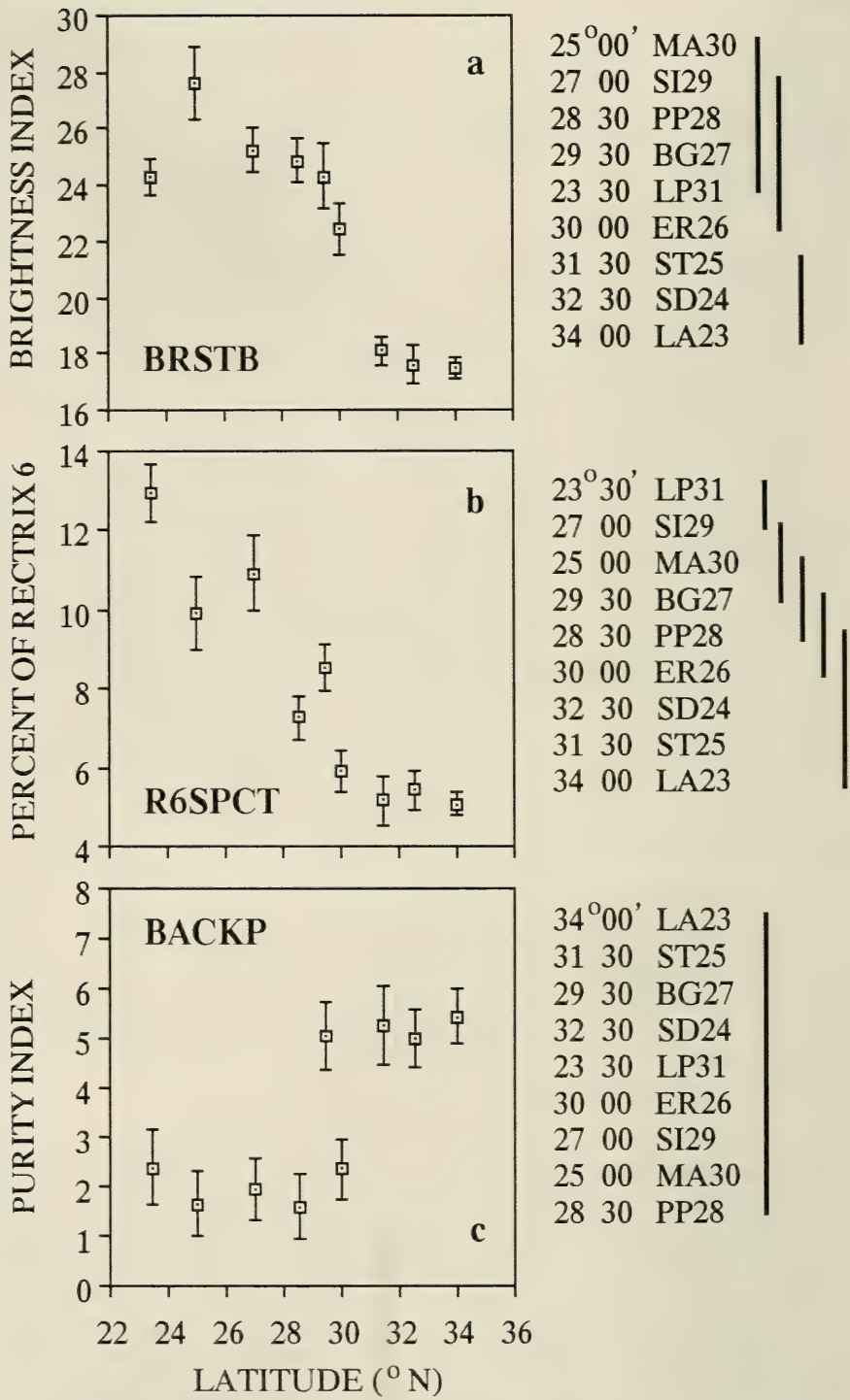


Fig. 3. Examples of geographic variation in characters included in Clusters 2 (BRSTB, BACKB, R5-6SL, R5-6SPCT, R5-6PCT, R5-6WEB) and 3 (BRSTW, BACKW, BACKP). See legend to Figure 2 for further explanation.

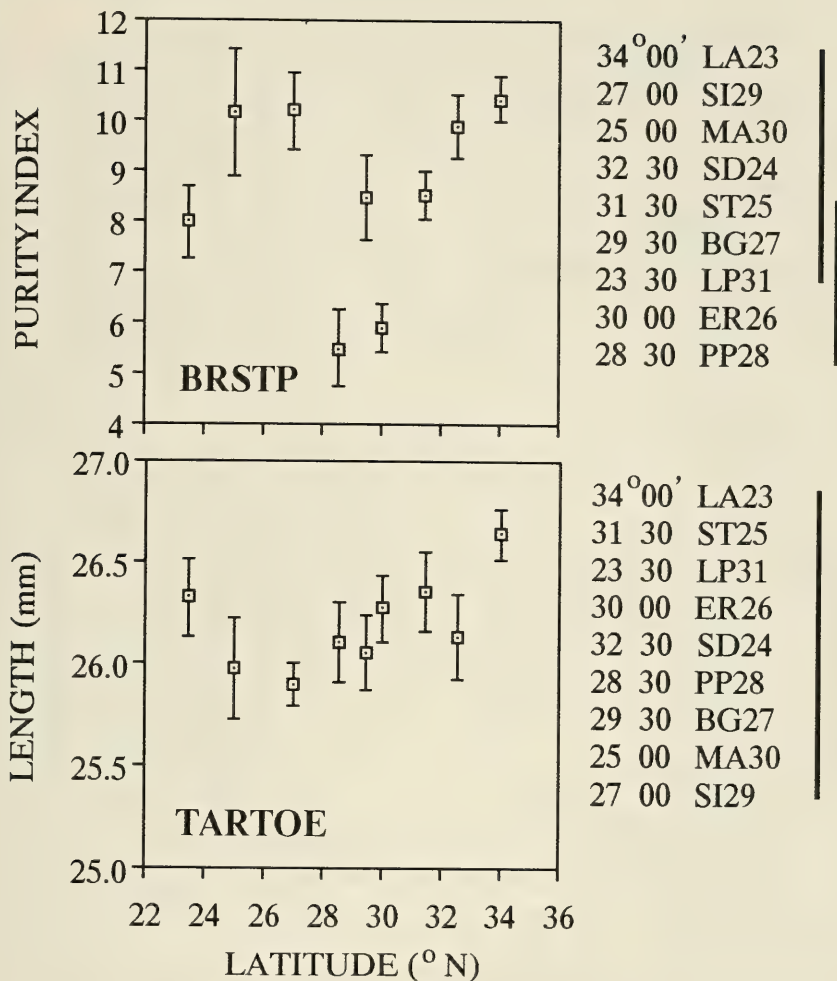


Fig. 4. Examples of geographic variation in characters included in Clusters 5 (BRSTP) and 6 (TARTOE). See legend to Figure 2 for further explanation.

4); in BRSTP, a sharp break in the pattern of variation occurred between 28°30'N and 27°N, and both characters showed some indication of a secondary step between 25°N and 23°30'N latitude. Clusters 4 (BWID, BDEP) and 7 (BLEN) showed no evident pattern of variation throughout the species' geographic range (Fig. 5).

To summarize similarities and differences among the 9 sample areas, I performed 2 UPGMA (unweighted pair-group method using arithmetic averages) cluster analyses using (1) 9 variables that were selected using stepwise discriminant function analysis ($P = 0.15$) as being those characters most effective in separating the 9 sample areas, and (2) 22 variables that had been used in a similar, multi-species analysis presented in Atwood (1988). Each of the resulting phenograms (Fig. 6) was structurally identical, with the principal dichotomy occurring between sample areas located north and south of 30°N latitude; a second major dichotomy also occurred between area LP31, located south of 25°N latitude, and other sample areas located south of 30°N latitude (MA30, SI29, PP28, BG27). Both phenograms

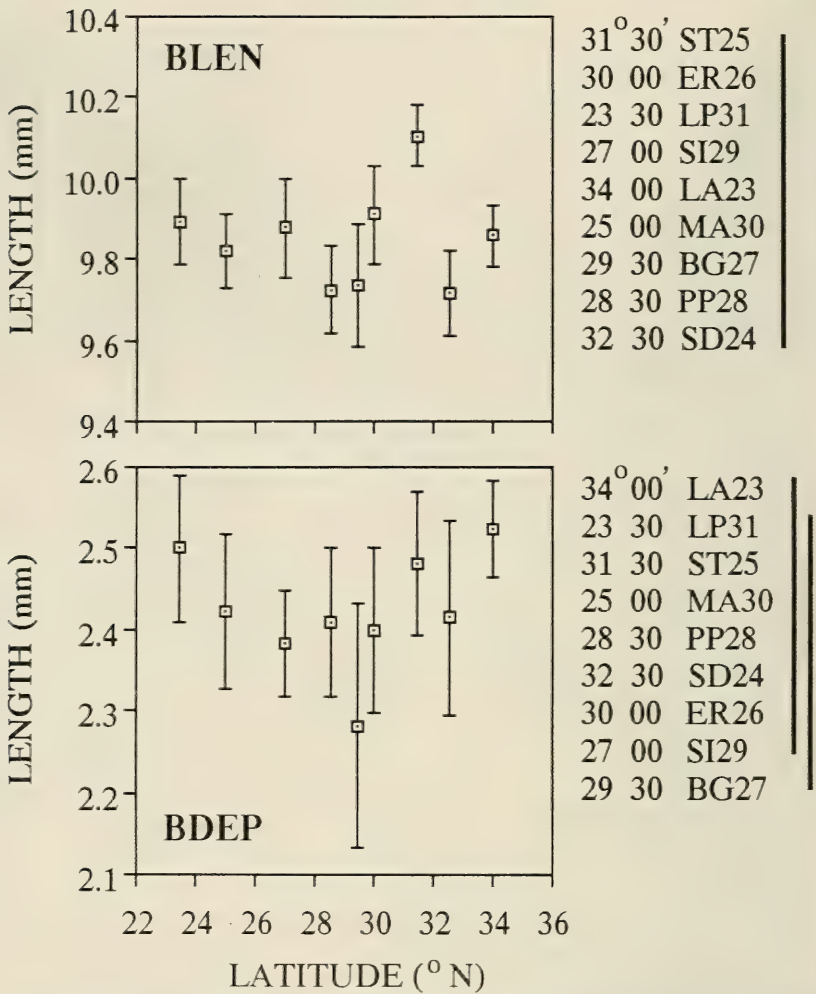


Fig. 5. Examples of geographic variation in characters included in Clusters 4 (BWID, BDEP), and 7 (BLN). See legend to Figure 2 for further explanation.

showed a markedly different cluster configuration than that derived from the multi-species analysis shown in Atwood (1988: 53).

To further examine the bases of these broad clustering patterns, for each character I compared differences between adjacent sample regions (Table 2). Eighteen of 31 characters were significantly different ($P < 0.05$, ANOVA) between Northern (north of 30°N latitude) and Central (30°N south to 24°N latitude) regions; included were most measurements of breast and back coloration, the amount of white present on rectrices 5 and 6, tail length, bill width and depth, and combined lengths of the tarsus and middle toe. Comparisons of samples from Central and Southern (south of 24°N) sections of Baja California showed significant differences in 15 characters, including measurements of wing length, bill width and depth, and the amount of white present on rectrices 5 and 6.

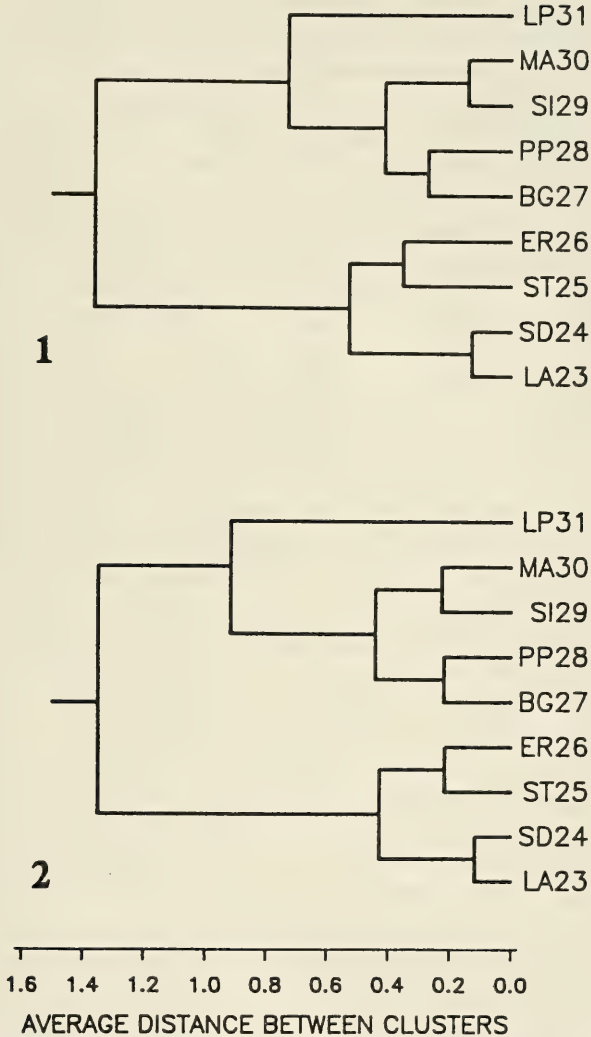


Fig. 6. Phenograms showing results of 2 UPGMA cluster analyses based on different combinations of morphological variables. Characters used in each analysis as follows: 1—BRSTB, BRSTP, BRSTW, BACKB, BACKP, P4LEN, R5SL, R5SPCT, R6WEB (variables selected using stepwise discriminant function analysis, $P = 0.15$); 2—BLEN; BWID; BDEP; TARTOE; P3-10LEN; R5-6WEB; TLEN; R4-6PCT; R5-6SPCT; R5-6SS (variables used in multi-species cluster analysis presented in Atwood (1988)).

Discussion

The taxonomy of *Polioptila californica* has had a rather tortured history. Most of the confusion has revolved around uncertainties concerning species limits (Atwood 1988). However, the relevant literature regarding subspecific nomenclature also includes various corrections, revisions, and ambiguities. Because these difficulties have been largely independent of taxonomic conclusions at the species level, for the sake of clarity I use the currently accepted species limits (American

Table 2. Comparison of character means in *Polioptila californica* between latitudinally adjacent regions defined by UPGMA clustering.

Char ^d	North ^a				Central				South		
	$\bar{x}$	SD	N	P ^b	$\bar{x}$	SD	N	P ^c	$\bar{x}$	SD	N
BLEN	9.87	0.51	110		9.80	0.45	58		9.89	0.52	25
BWID	2.69	0.27	109	***	2.48	0.21	57	***	2.77	0.23	26
BDEP	2.47	0.23	107	**	2.38	0.18	56	*	2.50	0.23	26
TARTOE	26.44	0.89	112	**	26.00	0.70	60		26.32	0.99	26
P3LEN	44.12	1.08	106		43.89	1.25	58		43.43	1.15	25
P4LEN	45.31	1.15	106		45.25	1.24	59	*	44.55	1.08	26
P5LEN	46.33	1.08	106		46.22	1.12	59	**	45.44	0.96	26
P6LEN	46.44	1.06	107		46.24	1.10	59	*	45.74	0.79	26
P7LEN	46.38	1.05	107		46.20	1.07	59	*	45.71	0.75	26
P8LEN	44.89	1.03	107		44.73	1.12	59	*	44.21	0.91	26
P9LEN	39.87	1.18	105		39.79	1.70	59		39.38	0.96	26
P10LEN	27.18	1.86	105		27.41	1.22	59		26.93	1.25	26
TLEN	49.51	1.42	104	***	48.53	1.71	55		47.88	1.28	24
R4LEN	47.86	1.54	102	**	47.07	1.85	55		46.34	1.35	23
R5LEN	45.77	1.55	102	**	45.05	1.74	54		44.51	1.62	23
R6LEN	40.43	1.61	105		40.25	1.58	55	*	39.04	2.64	23
R4PCT	0.97	0.01	102		0.97	0.01	55		0.97	0.02	23
R5PCT	0.92	0.02	100		0.93	0.01	54		0.93	0.02	23
R6PCT	0.82	0.02	103	***	0.83	0.02	55		0.82	0.05	23
R5WEB	0.12	0.06	107	***	0.19	0.16	56	*	0.30	0.16	24
R6WEB	0.58	0.14	111	***	0.81	0.16	57	***	0.96	0.12	26
R5SL	1.25	0.66	101	***	2.32	0.84	56	***	3.49	0.92	24
R6SL	2.66	1.06	111	***	4.48	1.48	57	***	6.37	1.87	24
R5SPCT	0.02	0.01	95	***	0.05	0.02	54	***	0.07	0.02	23
R6SPCT	0.05	0.02	104	***	0.09	0.03	55	***	0.13	0.03	23
BRSTB	18.36	3.33	98	***	25.41	2.74	32		24.28	3.01	22
BACKB	6.92	0.91	93	***	8.32	0.99	29		8.43	0.90	20
BRSTP	9.34	3.11	98	***	8.16	3.26	32		7.98	3.27	22
BACKP	4.87	3.31	93		2.31	2.15	29		2.38	3.38	20
BRSTW	576.92	1.72	98	***	574.94	3.05	32	*	576.71	2.82	22
BACKW	566.85	31.58	93	***	546.57	44.61	29		551.62	44.57	20

^a Sample areas (Fig. 1) grouped as follows: NORTH = LA23, SD24, ST25, ER26; CENTRAL = BG27, PP28, SI29, MA30; SOUTH = LP31.

^b Asterisks indicate significant differences (ANOVA) between NORTH and CENTRAL at $P < 0.05$ (*), 0.01 (**), or 0.001 (***).

^c Asterisks indicate significant differences (ANOVA) between CENTRAL and SOUTH at $P < 0.05$ (*), 0.01 (**), or 0.001 (***).

^d Character abbreviations as defined in Methods. Units in mm, except for (1) R4-6PCT, R5-6WEB, R5-6SPCT, which are proportions, and (2) BRSTB, BRSTP, BRSTW; BACKB, BACKP, BACKW, which are spectrophotometric indices calculated using procedures outlined by Judd (1933).

Ornithologists' Union 1989) in the following historical review, even though an author may have discussed a particular subspecies under a different specific name.

Polioptila californica, and thus the nominate subspecies, was originally described by Brewster (1881) on the basis of a specimen from Riverside, Riverside Co., California (34°N). Ridgway (1904) described what he apparently considered to be an insular subspecies, *margaritae*, based on two alcoholic specimens from Isla Santa Margarita, Baja California (Sur) (26°N). Later, Grinnell (1926) noted that birds from the nearby adjacent mainland at Bahía Magdalena were identical

to those of Isla Santa Margarita, and described the distribution of *margaritae* as extending latitudinally from 24°30' north to approximately 29°N. Grinnell (1926) considered *californica*'s southern distributional limit to be at El Rosario, Baja California (30°N), but specimens from the portion of the peninsula between 29° and 30°N latitude were lacking. Grinnell (1926) also described a third subspecies, *abbreviata*, based on 9 specimens from Cabo San Lucas, Baja California (Sur) (23°N); the distribution of *abbreviata* was considered to be from La Paz, Baja California (Sur) (24°N) south to Cabo San Lucas. Grinnell (1928) used an identical treatment, with the additional comment that "intergradation between the races *margaritae* and *californica* evidently takes place from 29° to 30° latitude;" similarly, *margaritae* and *abbreviata* were considered to intergrade near 24°30'N latitude.

Van Rossem (1931a), while concurring with Grinnell regarding "the number of races to be found in Lower California," disagreed "emphatically . . . on certain details of ranges." Based especially on the similarity of tail measurements between specimens from Isla Santa Margarita and areas south of La Paz, van Rossem (1931a) concluded that *abbreviata* was synonymous with *margaritae*; the northern range limit of this Cape region subspecies was not explicitly stated. Nonetheless, van Rossem (1931a) also recognized a "transitional form of the middle section of the peninsula," which he named *nelsoni*; this central Baja California subspecies was based on a type specimen collected at Bahía San Francisquito, Baja California (Sur) (28°30'N). Van Rossem (1931a) recognized that "the distribution of black-tailed gnatcatchers is probably continuous down the peninsula, but determination of the meeting place of *margaritae* and *nelsoni* must await further field work." Specimen localities cited for *nelsoni* included Bahía San Francisquito, Bahía Santa Teresa, Bahía Santa Ana, Santa Rosalía, San Lucas, San Bruno, San Ignacio, and Bahía San Bartolome (van Rossem 1931a). When van Rossem discovered that the name *nelsoni* was preoccupied by *Polioptila nelsoni* (Ridgway 1903), he renamed the central Baja California birds as *pontilis* (van Rossem 1931b).

The American Ornithologists' Union Check-List (1931, 1957) followed van Rossem's (1931a, b) basic outline of subspecies and their distributions. The subspecies *californica* was recognized as being resident "in southwestern California . . . south into northwestern Baja California, to about lat. 30°N." The range of *pontilis* was defined by the localities listed by van Rossem (1931a), thus extending only from approximately 28°30'N south to 27°N latitude; populations between the southern limit of *californica*'s range and the northern limit of the range of *pontilis* were not ascribed to any subspecies. The range of *margaritae* was given, apparently by default, as "from about lat. 27°N. south to the Cape District, including the islands of Santa Margarita and Espíritu Santo" (American Ornithologists' Union 1957).

The results presented here support retention of the currently recognized (American Ornithologists' Union 1957) distributional limits of *P. c. californica*, namely, from coastal southern California south to 30°N latitude in northwestern Baja California (Fig. 7). Univariate analyses indicate that a step occurs at this latitude in the measurements of several morphological characters, especially those related to darkness of body plumage and the amount of white on rectrices 5 and 6. Similarly, two multivariate cluster analyses produced identical principal groupings of sample areas: (1) areas LA23, SD24, ST25, and ER26, all located north of 30°N

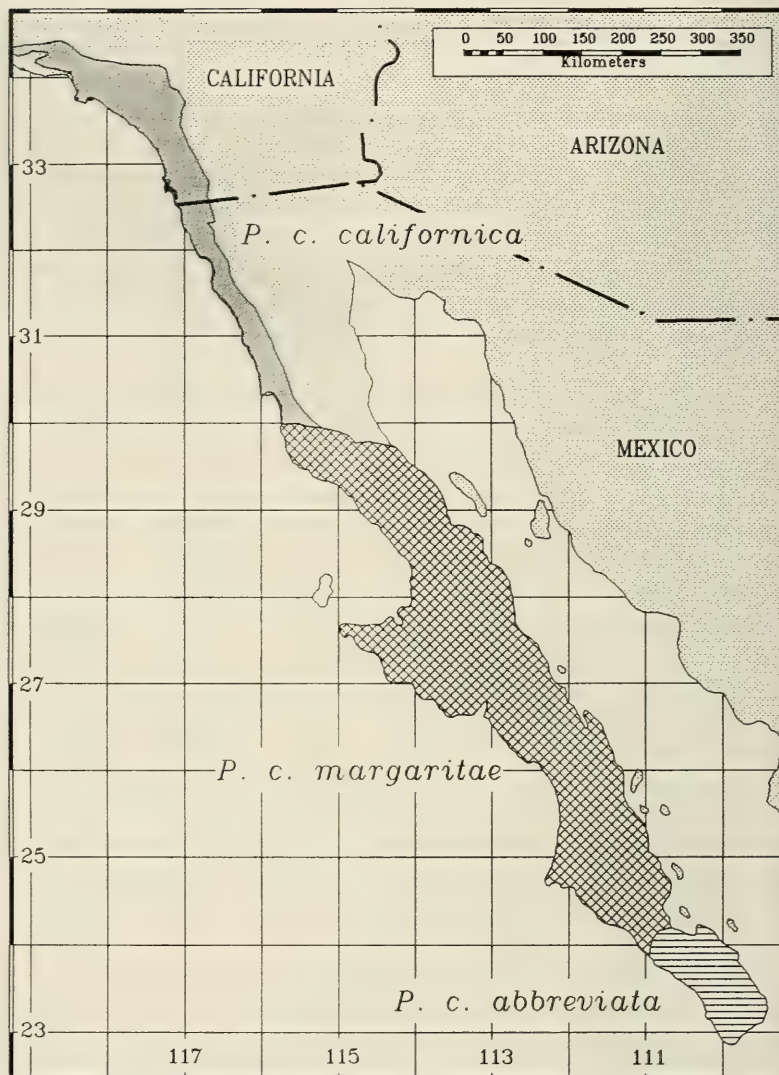


Fig. 7. Approximate geographic limits of California Gnatcatcher subspecies. Due to habitat loss, the indicated range of *P. c. californica* represents historic, not current, distribution. Mapped distributions of *P. c. margaritae* and *P. c. abbreviata* are similarly approximate, and include various areas characterized by habitat known to be unsuitable for California Gnatcatchers. For discussion of distributional patterns on islands in the Sea of Cortez, see Atwood (1988).

latitude, and (2) areas BG27, PP28, SI29, MA30, and LP31, all located south of 30°N latitude.

Populations of *Polioptila californica* occurring in central Baja California should therefore not be included within the subspecies *P. c. californica*, as I suggested earlier (Atwood 1988). My previous conclusion, that "two subspecies of *P. californica* would be reasonably recognized: *P. c. californica* in the northern portions of the species' range, and *P. c. margaritae* in the Cape region," was based (1) on visual inspection of geographic patterns of character variation using a method of

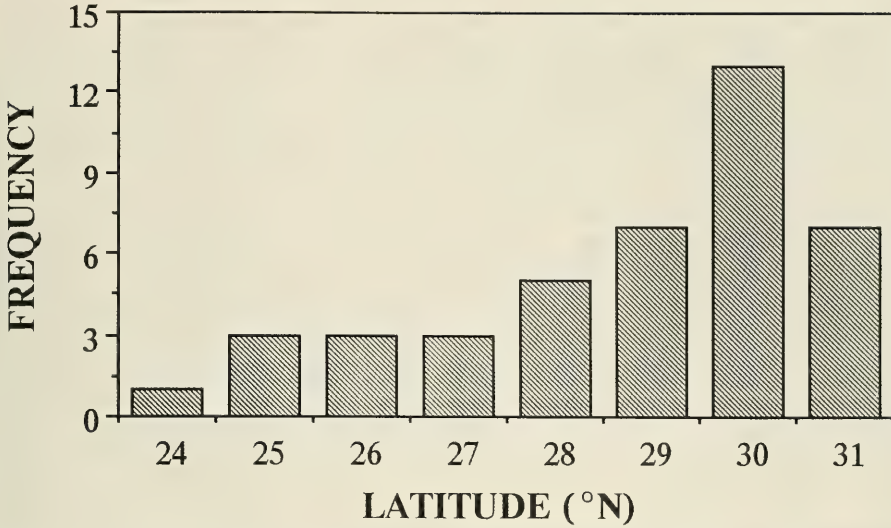


Fig. 8. Latitudinal location of subspecific or distributional transitions in lowland bird species of Baja California. Taxonomic and distributional information based on American Ornithologists' Union (1957) and Wilbur (1987). Species included in analysis: *Parabuteo unicinctus*, *Polyborus plancus*, *Falco sparverius*, *Callipepla californica*, *Zenaida asiatica*, *Otus kennicottii*, *Bubo virginianus*, *Micrathene whitneyi*, *Chordeiles acutipennis*, *Phalaenoptilus nuttallii*, *Hylocharis xantusii*, *Melanerpes uropygialis*, *Picoides scalaris*, *Colaptes auratus*, *Myiarchus cinerascens*, *Aphelocoma coerulescens*, *Auriparus flaviceps*, *Psaltiriparus minimus*, *Camphylorhynchus brunneicapillus*, *Thryomanes bewickii*, *Chamaea fasciata*, *Toxostoma cinereum*, *Toxostoma redivivum*, *Lanius ludovicianus*, *Cardinalis cardinalis*, *Cardinalis sinuatus*, *Passerina versicolor*, *Pipilo fuscus*, *Aimophila ruficeps*, *Spizella atrogularis*, *Amphispiza bilineata*, *Amphispiza belli*, *Carpodacus mexicanus*. Species primarily restricted to montane habitats or to the Colorado Desert region of northeastern Baja California, as well as species lacking subspecific variation in Baja California, are excluded.

data presentation that has been rightly criticized by Banks (1989), and (2) the results of a cluster analysis that, by simultaneous inclusion of three species (*Poliophtila californica*, *Poliophtila melanura*, and *Poliophtila nigriceps*), obscured important aspects of intraspecific variation. Correct examination of the same data indicates that populations of *Poliophtila californica* north of 30°N latitude are suitably distinct to warrant taxonomic recognition at the subspecific level from populations south of this latitude, and that it would be inappropriate to consider the range of *P. c. californica* as extending south of 30°N latitude.

Analysis of geographic distributions and subspecific limits of 33 other resident bird species occurring in the arid, lowland regions of Baja California indicates that 30°N occurs more frequently than any other latitude as a boundary in these distributional or taxonomic limits (Fig. 8). Latitude 30°N represents the southern terminus of the coastal sage scrub plant community (O'Leary 1990), and consequently marks an important transition zone for various arid-land components of the Baja California biota, including plants (Shreve 1936; Shreve and Wiggins 1964; Wiggins 1980), terrestrial insects (Truxal 1960; Brown 1987), land mammals (Orr 1960), reptiles (Savage 1960; Murphy 1983) and scorpions (Williams 1980; Murphy 1983).

South of 30°N latitude, California Gnatcatchers show mostly clinal patterns of

variation, with variably pronounced steps in different characters occurring near 28°N and/or 24°N. Multivariate analysis identifies 24°N as the primary zone of morphological change in central and southern Baja California, with no indication that 28°N latitude is a comparably important transition. These results suggest that two subspecies of California Gnatcatcher should be recognized in the central and southern portions of Baja California, with the zone of intergradation between these forms being located near 24°N latitude (Fig. 7).

This conclusion agrees with Grinnell's (1926, 1928) original assertion that the northern limit of the Cape region subspecies is located near 24°30'N latitude, and contradicts van Rossem's (1931a) revision that was based on the similarity of birds from Isla Santa Margarita to those from areas of the Cape region near Cabo San Lucas and La Paz. Consequently, the subspecific nomenclature of California Gnatcatchers south of 30°N latitude should properly revert to that initially proposed by Grinnell (1926), with *P. c. margaritae* being distributed in central Baja California from 30°N south to 24°N, and *P. c. abbreviata* occurring in the Cape region of Baja California south of 24°N latitude. It is unfortunate that the name *abbreviata* was originally given by Grinnell in reference to the short tail of the type specimens because, as correctly noted by van Rossem (1931a), variation in this single character actually shows its most pronounced step near 28°N rather than at *abbreviata*'s northern limit near 24°N latitude.

The existence of three subspecies of California Gnatcatchers south of 30°N latitude might conceivably be argued, with transitions located at both 28°N and 24°N. In this approach, central Baja California populations north of 28°N would be distinguished from those south of this latitude on the basis of tail length, and a combination of plumage coloration characters would separate populations north and south of 24°N latitude. Alternatively, a single, somewhat variable subspecies, characterized by incongruent patterns of variation among different morphological characters, might be recognized as occurring south of 30°N latitude. That is, cluster dichotomies other than the major separation of populations located north and south of 30°N latitude might be considered taxonomically insignificant.

Based on available data, I see no compelling reason to follow either of these interpretations, although additional specimen material may ultimately require further taxonomic analysis. Also, as noted by Atwood (1988), the taxonomic status of California Gnatcatchers on Isla Espíritu Santo (25°N), Isla San José (24°30'N), and possibly other islands in the Sea of Cortez remains uncertain due to lack of adequate specimen material.

In summary, I recommend that the subspecific limits, distributions and characteristics of *Polioptila californica* be described as follows. Descriptions are based on alternate-plumaged males. Measurements represent the mean values of specimens examined in the present study. Plumage color notations refer to standards provided by Munsell Products (1973); colors of soft parts are based on comparisons with Smithe (1975).

P. c. californica Brewster.—Resident from coastal southern California south into northwestern Baja California to approximately 30°N latitude. Distinguished from other subspecies by darker body plumage, less extensive white on rectrices 5 and 6, and longer tail. *Type Locality*: Riverside, San Bernardino [=Riverside] Co., California (Brewster 1881). *Measurements (mm)*: Wing length (unflattened chord): $\bar{x}$ = 46.4 (S.D. = 1.1, range 44.0–49.0, N = 107); tail length: 49.5 (1.4,

46.4–53.2, 104); exposed culmen: 9.9 (0.5, 8.5–11.3, 110); tarsus + middle toe: 26.4 (0.9, 24.0–29.1, 112). *Plumage Coloration*: Underparts dark gray (7.5Y, 5/0), becoming slightly paler on throat, center of abdomen and undertail coverts; upperparts, including hindneck, back, scapulars, lesser wing coverts and rump very dark gray (7.5YR, 3/0). Wing dark brownish (7.5YR, 3/2), with leading edges of primaries and secondaries edged with pale gray. Crown uniform glossy black; white eyering incomplete, usually limited to area below eye. Upper tail coverts and rectrices 1–4 black; rectrix 5 mainly black, tipped with approximately 1 mm of white and with outer vane showing very limited or no white edging; rectrix 6 mainly black, tipped with approximately 2 mm of white and with outer 50 percent of outer vane white; shape of tail spot on rectrices 5 and 6 such that length of white from feather tip along shaft is less than from feather tip along inner vane. *Soft Parts Coloration*: Maxilla black (Color 82); tip of mandible black (Color 82), becoming paler gray (Color 84) at base; tarsus blackish, intermediate between Colors 82 and 83; foot pad pale brownish-gray, intermediate between Colors 79 and 80.

P. c. margaritae Ridgway.—Resident in central Baja California from 30°N south to approximately 24°N latitude including, tentatively, Isla Espíritu Santo and Isla San José. Distinguished from *californica* by paler body plumage, more extensive white on rectrices 5 and 6, shorter tail, smaller bill width and depth, and shorter length of tarsus + midtoe; from *abbreviata* by paler body plumage, less extensive white on rectrices 5 and 6, longer wings, and smaller bill width and depth. *Type Locality*: [Santa] Margarita Island, [Baja California (Sur)] (Ridgway 1904). *Measurements (mm)*: Wing length: (unflattened chord), 46.2 (1.1, 43.5–48.7, 59); tail length: 48.5 (1.7, 45.5–51.9, 55); exposed culmen: 9.8 (0.5, 8.6–11.0, 58); tarsus + middle toe: 26.0 (0.7, 24.3–27.5, 60). *Plumage Coloration*: As in *californica* with following exceptions. Underparts light gray (7.5YR, 6/0); upperparts dark gray (7.5Y, 3.5/0). White eyering varying from partial (below eye) in the north to nearly complete or complete in the south. Rectrix 5 tipped with approximately 2 mm of white and with outer 20 percent of outer vane white; rectrix 6 tipped with approximately 4 mm of white and with outer vane mostly white. *Soft Parts Coloration*: As in *californica*.

P. c. abbreviata Grinnell.—Resident in southern Baja California from 24°N latitude south throughout the Cape region. Distinguished from *margaritae* by more extensive white on rectrices 5 and 6, shorter wings, and larger bill width and depth; from *californica* by shorter tail and wings, paler body plumage, and more extensive white on rectrices 5 and 6. *Type Locality*: Cape San Lucas, Baja California (Grinnell 1926). *Measurements (mm)*: Wing length (unflattened chord), 45.7 (0.8, 43.9–47.2, 26); tail length, 47.8 (1.3, 45.1–50.7, 24); exposed culmen, 9.9 (0.5, 8.8–10.9, 25); tarsus + middle toe, 26.3 (1.0, 23.6–29.1, 25). *Plumage Coloration*: As in *californica* with following exceptions. Underparts light gray (7.5YR, 6.5/0), becoming slightly paler on throat, center of abdomen and undertail coverts. White eyering complete or nearly so. Rectrix 5 tipped with approximately 3 mm of white and with outer 20 percent of outer vane white; rectrix 6 tipped with approximately 6 mm of white and with outer vane mostly or entirely white; shape of tail spot on rectrices 5 and 6 such that length of white from feather tip along shaft is usually longer than from feather tip along inner vane. *Soft Parts Coloration*: As in *californica*.

Acknowledgments

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ANNOUNCEMENT

"INTERFACE BETWEEN ECOLOGY AND LAND DEVELOPMENT IN CALIFORNIA"

This will be the title of a symposium to be held at the annual meeting of the Southern California Academy of Sciences, 1-2 May 1992 at Occidental College in Los Angeles. The meeting will begin Friday morning with a plenary address by Dr. Peter Raven, followed by morning and afternoon sessions on both Friday and Saturday. It is anticipated that the symposium will consist of four sessions on: Biodiversity and Habitat Loss, Mitigation of Development, Restoration of Damaged Communities, and Wildlife Corridors. The focus of the meeting is to bring together persons involved in basic research, applied environmental consulting, and governmental policy. Persons interested in participating or suggestions for related sessions should contact: Dr. Jon Keeley, Department of Biology, Occidental College, Los Angeles, California 90041; 213-259-2958 (fax).

Research Notes

Geographic Ranges of Recent Hermatypic Coral Genera in Baja California Sur, Mexico

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The eastern Pacific Ocean hermatypic coral fauna occurs on the west coast and offshore islands of Mexico, Central America, and South America. Its southern limit in the Galapagos Islands was carefully studied by Glynn and Wellington (1983). The northern limit in northwestern Mexico is broadly known and has been described by Squires (1959) and Reyes (1990), among others. In this region, due to the existence of the Baja California peninsula, the north-trending coastline of Mexico abruptly reverses direction at the Colorado River delta to follow the Baja California peninsula south, and at about 80 km south of the Tropic of Cancer it turns north again. The hermatypic coral fauna follows this geographic sigmoid flexure along much of the east and west coasts of the Gulf of California, with its extreme end range represented by one genus that continues up the west side of the peninsula, an area chiefly occupied by a temperate, non-hermatypic, coral fauna.

In the Gulf of California, the hermatypic coral fauna comprises five genera: *Cycloseris*, *Pavona*, *Pocillopora*, *Porites*, and *Psammocora*. Details of the occurrence and distribution of these genera in the southern portion of Baja California, where Wilson (1988) discovered *Pocillopora* significantly beyond the previous reported end range, have not been documented. In April 1990, a survey of this coast was undertaken to rectify the lack of knowledge. The results of that inventory are presented here as reports of the geographic end range localities for each genus (summarized in Fig. 1, which also shows most place names mentioned in the text) and a brief discussion of some salient related observations. The genera classically drop out one-by-one along the coast as they do elsewhere in the world.

All five genera occur in the well-known area of reefs at Bahía Pulmo and northward into the Gulf of California. *Cycloseris* was not encountered southwest of Bahía Pulmo. At Bahía Santa Maria, four genera are still present: *Pocillopora* (very common, large coralla), *Porites* (moderately common, encrusting), *Pavona* (uncommon), and *Psammocora* (rare, small coralla). At Playa Barco Varado, three genera are still present: *Pocillopora* (common, large coralla), *Porites* (moderately common, encrusting and *Pavona* (rare). At Cabo San Lucas, only two hermatypic genera occur: *Pocillopora* and *Porites*, both represented by coralla that become progressively rarer and smaller in the short distance between the islands near the harbor entrance and the islands at the tip of the cape. The non-hermatypic tropical coral *Tubastrea* also is present on an island near the harbor, which is the end of its range (Wilson 1990).

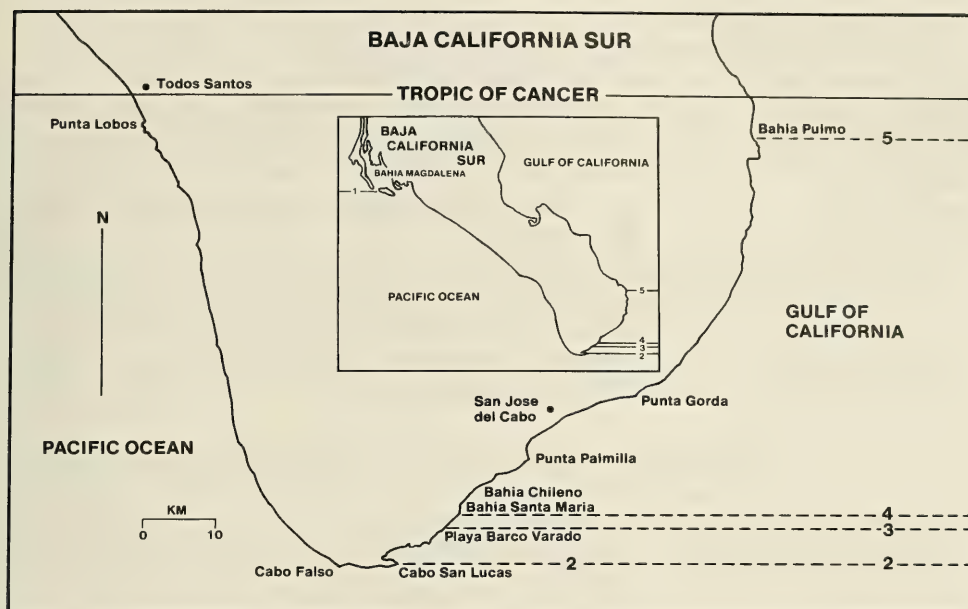


Fig. 1. Map of southern coast of Baja California Sur, Mexico, showing locations of place names mentioned in text and numbers indicating quantity of hermatypic coral genera present. Inset map at smaller scale includes location of the one living hermatypic coral genus on the west coast of the Baja California peninsula in relation to the other isorhythms. The genera present at the numbers are, 5: *Cycloseris*, *Pavona*, *Pocillopora*, *Porites*, *Psammocora*; 4: *Pavona*, *Pocillopora*, *Porites*, *Psammocora*; 3: *Pavona*, *Pocillopora*, *Porites*; 2: *Pocillopora*, *Porites*; 1: *Porites*.

Pavona and *Psammocora* were not previously known to range southwest of Bahía Pulmo.

West of Cabo San Lucas and north up the Pacific coast, the only living hermatypic coral present is *Porites* (see Wilson 1988 and Reyes 1990 for comments on table 3 of Squires 1959), which was first reported by Squires (1959) in Bahía Magdalena on the southernmost island.

The only true reefs seen southwest of Bahía Pulmo in the course of this study were small ones near the low islands in Bahía Chileno, where *Pavona* and *Pocillopora* coralla are intergrown to form build-ups, assisted somewhat by moderately large, nodular coralla of *Porites*. Southwest of Bahía Chileno, living *Porites* coralla all are encrusting, although nodular coralla of uncertain age in the dredge spoil heaps at Bahía San Lucas harbor indicate that they once lived there.

The reefs at Bahía Chileno and the associated reef fauna (including the coral-livore starfish *Acanthaster*) seem nearly as luxuriant as those of Bahía Pulmo and deserve to be studied further.

The primary substrate available for all the corals at the localities examined was granite, with the exception of some sandstone along a short stretch of coast east of Punta Gorda. The substrate for the corals at Bahía Pulmo likewise is granite, although in places on shore it is overlain by a coral-bearing Upper Pleistocene cobble conglomerate, which also may occur underwater in some parts of the area. The sands of all beaches examined generally are coarse-grained and granite derived but at Bahía Chileno there is some admixture of coral sand.

Searches of several headlands on the west coast of Baja California Sur disclosed no hermatypic corals between Bahía Magdalena and Cabo San Lucas. A particularly careful search was made at Punta Lobos, south of Todos Santos, where habitats possibly amenable to hermatypic corals appeared to exist. Cabo Falso, the southernmost point on the Baja California peninsula (about 5 km west and slightly south of Cabo San Lucas), was not searched because of dangerous water conditions, but it extends only a short distance into the sea and appears to offer little potential habitat for hermatypic corals.

Voucher specimens collected during this survey were deposited in the Invertebrate Zoology Section, Natural History Museum of Los Angeles County. They are accompanied by species identifications made by Hector Reyes. Permission to collect was granted by the Universidad Autonoma de Baja California Sur, La Paz, through the courtesies of Jorge Garcia Pamanes and Oscar Arizpe of that institution.

A number of people assisted with the survey. I wish especially to thank Hector Reyes for his expert assistance in every phase. Michael Lewis generously photographed many occurrences. Field assistance was provided by them and by Barbara Dahn, Harold Elliott, Gordon Hendler, Peggy McCain, Jack Nault, Florence Nishida, Raul Rodriguez, LouElla Saul, Richard Saul, Judith Smith and Lauren Tawa. Mary Butler prepared the figure. J. Wyatt Durham generously reviewed an early manuscript.

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COVER: In situ photograph of new species of purple jellyfish, *Chrysaora* sp., taken by member of Howard Hall film crew off Coronado Norte, Islas de Los Coronados, Northern Baja California, México, July 1989. See page 89.